A perspective on the seed bank dynamics of *Acacia saligna*

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Thesis presented in partial fulfilment of the requirements for the degree Master of Science in Conservation Ecology at the University of Stellenbosch

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March 2012

Declaration

By submitting this thesis/dissertation electronically, I declare that the entirety of the work contained therein is my own, original work, and that I have not previously in its entirety or in part submitted it for obtaining any qualification.

Signature: _____ Date: March 2012

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Abstract

Acacia saligna, or Port Jackson, is an Australian *Acacia* which has spread throughout the Western and Eastern Cape provinces of South Africa where it has become invasive and a prominent feature of the vegetation. In areas where *A. saligna* establishes it replaces natural vegetation, alters ecosystem processes and interferes with agricultural practices. Consequently large management efforts have been made to eradicate this invasive alien tree. However, its large and persistent soil stored seed bank, even in the presence of management and biological control agents, poses a serious obstacle to its successful removal. Furthermore the reproductive output and the size of the seed bank of *A. saligna* over its whole distribution as well as the variation of seed production and the seed bank with environmental conditions in time and space is poorly known. Understanding the seed bank dynamics of *A. saligna* in time and space is essential for reducing invasive success and achieving management objectives. This study has filled this knowledge gap through studying the seed production and seed bank of *A. saligna* over its invaded range in South Africa, including how environmental factors influence these factors in time and space. The seed rain of *A. saligna* was assessed at 10 sites across its distribution in South Africa. The seed rain of *A. saligna* at the sites was determined through the use of seed rain traps. Twenty five traps were placed out at every site during November 2010 (pre-dehiscence) which was collected again during April 2011 (post-dehiscence). The seed bank of *A. saligna* was estimated through sampling at 25 sites across its distribution range in South Africa. The seed bank was sampled during April 2010 (post-dehiscence), November 2010 (pre-dehiscence) and April 2011 (post-dehiscence) through taking 50 litter and soil samples at every site which gave a total sampling size of 3 750 for both the seed in the soil and litter over its distribution in South Africa. In addition the average tree diameter, tree density, average number of *Uromycladium tepperianum* induced galls per tree, the summer aridity index, De Martonne aridity index, winter concentration of precipitation, temperature of coldest month and the soil texture for every site was determined. The damage done by the seed feeding weevil, *Melanterius compactus*, was also estimated for the seed rain study sites. Water availability during the hot summer months was assessed as the most important factor governing seed production and seed bank size. Riparian and non-riparian water regimes were shown to be important in understanding the seed bank dynamics of *A. saligna* over its distribution range in the Cape Floristic Region. In non-riparian *A. saligna* populations the seed production and consequently the size of the seed bank and its rate of accumulation is limited by both water and temperature and in riparian *A. saligna* populations, only by temperature. Therefore, two environmental gradients influence the seed bank dynamics of Port Jackson in South Africa. In non-riparian *A. saligna* populations the number of seed produced and the accumulation of seed in the seed bank generally increases along the west coast of South Africa from Clanwilliam towards Cape Town and along the south coast from Cape Town towards Port Elizabeth. Seed banks are larger closer to the coast, when *A. saligna* populations of similar age are compared. In riparian *A. saligna* populations, the

number of seed produced generally increases from Port Elizabeth towards Cape Town and from Cape Town towards Clanwilliam, again, with larger seed banks being accumulated closer to the coast, when populations of similar age are compared. This study provides managers with a useful tool for prioritising management efforts.

Opsomming

Acacia saligna of Port Jackson is ‘n indringerplant in Suid-Afrika wat afkomstig is uit Suid-Wes Australië. *Acacia saligna* is ‘n onmisbare kenmerk van die plantegroei in die Wes en Oos-Kaap. Waar Port Jackson vestig, verplaas dit natuurlike plantegroei, verander dit ekosisteem prossesse en verhinder dit landbou praktyke. Gevolglik is groot bestuurspogings aangewend om hierdie indringer plant uit te roei. In die teenwoordigheid van bestuursprogramme en biologiese beheer bly *A. saligna* lewensvatbaar as ‘n gevolg van die plant se groot blywende grond saadreserwes. Verder is die saad produksie en saadbank grootte van *A. saligna* oor sy verspreiding bereike asook hoe dit met omgewingstoestande in tyd en ruimte interreageer en varieer grootendeels onbekend. ‘n Goeie en omvattende begrip van die saadbankdinamika is belangrik om die indringings vermoë van die plant te verlaag en om bestuursdoelwitte te bereik. Hierdie studie vul die bestaande gaping in die kennis aangaande die saadbank dinamika van *A. saligna* aan deur die saadproduksie en die saadreserves van die indringerplant oor sy verspreiding in Suid-Afrika te bestudeer, insluitend hoe omgewingstoestande die saadbankdinamika beïnvloed in tyd en ruimte. Die saadreën vir 10 *A. saligna* populasies was bepaal deur die gebruik van saadlokvalle. Vyf-en-twintig lokvalle was uitgeplaas in elke bestudeerde Port Jackson perseel gedurende November 2010 (voor-saadval) wat weer gaan haal is gedurende April 2011 (na-saadval). Die saadbank van *A. saligna* was bepaal in 25 populasies van die boom gedurende April 2010 (na-saadval), November 2010 (voor-saadval) en April 2011 (na-saadval) deur die neem van 50 blaar- en grondmonsters by elke perseel wat ‘n totaal van 3 750 blaar- en grondmonster gee oor die hele verspreiding van *A. saligna* in Suid-Afrika. Verder is die gemiddelde boomdeursnee, boomdigtheid, gemiddelde *Uromycladium tepperianum* geinduseerde galle per boom, die somers droogtheids indeks, De Martonnes droogtheids indeks, die winter konsentrasie van presipitasie, die temperatuur van die koudste maand en die grond tekstuur van elke Port Jackson stand bepaal. Die skade wat die saad voedende kewer, *Melanterius compactus,* aanrig aan die sade van *A. saligna* is ook vir die persele waar die saadreën eksperiment uitgevoer is, bepaal. Die beskikbaarheid van water vir *A. saligna* in die droë somermaande is bepaal as die belangrikste faktor wat die grootte van die saadproduksie en saadbank beïnvloed. Oewer en nie-oewer water omgewings is bevind as noodsaaklik om die saadbank dinamika van *A. saligna* oor die indringerplant se verspreidingareas in die Kaap Floristiese Streek te verstaan. In nie-oewer *A. saligna* populasies word saadproduksie en gevolglik die grootte en tempo van akkumulasie van die saadbank deur beide water en temperatuur omstandighede beperk, terwyl in oewer *A. saligna* populasies word die indringerplant slegs deur temperatuur omstandighede beperk. Gevolglik blyk dit dat twee water beskikbaarheids gradiënte bestaan waarop die plant reageer wat dan uitgedruk word in die plant se saad produksie en gevolglik ook die plant se saadbank. In nie-oewer Port Jackson populasies neem die saadproduksie en die tempo waarteen die saadbank akkumuleer algemeen toe langs die weskus van Clanwilliam na Kaapstad en van Kaapstad na Port Elizabeth, met grootter saadproduksie en

saadbank akkumulasie nader aan die kusgebiede, wanneer *A. saligna* populasies van dieselfde ouderdom vergelyk word. In oewer Port Jackson populasies neem die saadproduksie en die tempo waarteen die saadbank akkumuleer algemeen toe van Port Elizabeth na Kaapstad en van Kaapstad na Clanwilliam, met grootter saadproduksie en saadbank akkumulasie nader aan die kusgebiede, wanneer *A. saligna* populasies van dieselfde ouderdom vergelyk word. Hierdie studie verskaf bestuursplanne met ‘n nuttige raamwerk waarvolgens uitroeiing en beheer programme vir *A. saligna* beplan kan word.

Acknowledgements

My heavenly Father through which all things are possible

I would like to acknowledge and thank the following persons and institutions:

The Centre for Invasion Biology for funding my project and for the opportunity to better myself.

My supervisors Prof. Karen J. Esler and Dr. Alan R. Wood for their guidance, help and assessment of my work.

All the land managers that allowed me to work on their land.

Weather SA and the ARC-ISCW for allowing me to use their weather data.

The soil science department of the University of Stellenbosch for analysisng my soil samples

Mr. M. Ngwenja (ARC) for doing my GLMMs statistical analysis.

Dr. R. Veldman, Mr. H. Nottebrock and Dr. J.R.U. Wilson for their help with my statistical analysis.

Ms J. Moore and F.A.C. Impson for their advice and help with the design of the seed rain traps.

Ms. M. Wenn and Mr. E. Scholtz for their technical assistance and friendly help.

Dr. G.J. Strydom, Mr. J.G. Strydom and Mr. J.E.F. Smith for helping me with my fieldwork.

My mother, father, brother and sister for their support and encouragement.

My classmates and friends in the department, especially Marko, Megan, Martina, Lelani and Henning.

Aan my Oupa

Ds. J.G. Odendaal wat altyd ‘n goeie storie en grappie gehad het.

Psalm 121

Op pad

‘n Bedevaartslied

Ek slaan my oë op na die
berge: waar sal my hulp vandaan
kom?
My hulp is van die Here wat
hemel en aarde gemaak het.
Hy kan jou voet nie laat
wankel nie; jou Bewaarder kan nie
sluimer nie.
Kyk, die Bewaarder van Israel
sluimer of slaap nie.
Die Here is jou Bewaarder;
Die Here is jou skaduwee aan jou
regterhand
Die son sal jou bedags nie
steek nie, die maan ook nie by nag
nie.
Die Here sal jou bewaar vir
elke onheil; jou siel sal Hy bewaar.
Die Here sal jou uitgang en jou ingang
bewaar, van nou af tot in ewigheid.

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Introduction

Rationale

Alien plants are a problem of national and global significance (Van Wilgen *et al*., 2001). Their impacts (reduced biodiversity, decreased water availability etc.) cause damage amounting to billions of dollars annually (Van Wilgen *et al*., 2001). In South Africa approximately 201 alien species cover approximately 10 million hectares or 8.6 % of the country's total land surface (Le Maitre *et al*., 2000) and are a cause for ecological and economic concern in natural and semi-natural systems (Nel *et al*., 2004). Many of these species, including the worst of these weeds, are native to Australia (Shaugnessy *et al*., 1978). The Western Cape has the greatest level of invasion with about 28.82 % of its surface covered (Le Maitre *et al*., 2000; Henderson, 2007).

The botanically rich Western Cape, home to a major part of the Cape Floristic Region (CFR) (Goldblatt, 1997) is a province of South Africa that is also host to the most alien plants. The CFR harbours one of six plant kingdoms globally (Van Wilgen *et al*., 1996) and has been selected as one of the world's significant areas for conservation action (Cowling and Heijnis, 2001; Cowling *et al*., 2003). In addition to being renowned for its high species richness and endemism (Goldblatt and Manning, 2000; Goldblatt and Manning, 2002), the CFR creates 25 000 job opportunities and generates R 80 000 million annually (estimated in 1993) through cut and dried flowers industries (Binns *et al*., 2001). Invasive alien plants (IAPs) constitute the greatest threat, after urbanisation and agriculture, to the unique vegetation of the CFR (Binns *et al*., 2001), endowing numerous taxa with the status of being endangered or threatened (Van Wilgen *et al*., 1996; Raimondo *et al*., 2009). Therefore, in the Western Cape alien plants not only pose a threat to biodiversity, ecosystem character and function, but also negatively impact society by reducing resources critical for human well being.

In South Africa approximately 70 species of Australian *Acacia* have been introduced (Richardson *et al*., 2011) over the last 200 years (Shaugnessy *et al*., 1978), of which 14 have become invasive (Richardson *et al*., 2011). Invasive Australian Acacias cover about 554 000 hectares of the country's surface (Van Wilgen *et al*., 2011). *Acacia mearnsii*, *A. saligna*, *A. cyclops* and *A. dealbata* are in the top ten of the fifty most problematic and widely distributed species in South Africa (Henderson, 2007). Furthermore in the Western Cape *A. mearnsii* and *A. saligna* are ranked as the top two invaders (Henderson, 2007) with *A. saligna* being the most damaging invasive species in the coastal lowlands of the south-western Cape (Macdonald and Jarman, 1984; Van Wilgen and Richardson, 1985).

Acacia saligna has formed large dense stands over a vast area in the west, south and eastern coastal regions on conservation, water catchment and agricultural land (Morris, 1997; 1999). This

has resulted in the replacement of natural vegetation, alterations in ecosystem processes and interference with agricultural practices (Morris, 1997; 1999). There are few areas where *A. saligna* populations are actively being managed as mechanical and chemical control of Port Jackson trees are both costly (Morris, 1991). Consequently these control efforts have only been focused in valuable conservation and intensively farmed areas (Morris, 1991). However, even in the areas where it is being managed, the ability of *A. saligna* to accumulate persistent seed banks prevents its effective and sustained removal (Richardson and Kluge, 2008; Wilson *et al*., 2011).

To increase the effectiveness of control operations on *A. saligna* over its entire distribution, the Australian gall inducing rust fungus, *Uromycladium tepperianum,* was released as a biological control agent into South African populations (Morris, 1997; 1999). *Uromycladium tepperianum* results in decreased stand density (to 5 – 10 % of original stand density) (Morris, 1999), reduced canopy density and reduced seed production (Wood and Morris, 2007). In addition a seed-feeding weevil, *Melanterius compactus,* was introduced into naturalized *A. saligna* populations in South Africa to further reduce seed production (Wood and Morris, 2007; Impson *et al*., 2011). *Melanterius compactus* is the most successful weevil of all the *Melanterius* species released in South Africa as biological control agents (Impson *et al*., 2011). Where it has established, *M. compactus* is observed as considerably reducing seed rain and is described as having damage levels of 90 % regularly (Impson *et al*., 2011).

Even with the highly detrimental effects of *U. tepperianum* and *M. compactus* on *A. saligna*, seed production is still high enough to lead to the accumulation of large numbers of viable seed in the seed bank and therefore may still be great enough to maintain high levels of recruitment, creating a cause for concern (Strydom *et al*., 2012). Seed banks enable *A. saligna* to survive in time and space and to re-establish in an environment that may temporarily be free from biological control agents and management. Seed rain for Port Jackson populations has been recorded to be between 446 and 13 472 seeds m^{-2} (Wood and Morris, 2007) while seed bank density in southern Africa has been recorded as being between 2 000 seeds m^{-2} (Morris, 1999) and 212 000 seeds m^{-2} (Morris, 1997). Most of *A. saligna* seed are viable (86 – 100 %) (Milton and Hall, 1981; Holmes *et al*., 1987). The rate of seed accumulation increases with tree age until the trees reach an age of approximately 30 years whereafter seed accumulation rates stabilize (Milton and Hall, 1981). *A. saligna* seed banks have a clumped horizontal distribution (Strydom *et al*., 2012) with the largest proportion of seed being situated below the litter but within the upper 10 cm of the soil (Milton and Hall, 1981; Strydom *et al*., 2012). The number of seed in the soil decreases with depth and below 10 cm soil depth the number of seed declines rapidly (Milton and Hall, 1981; Strydom *et al*., 2012).

In order to manage *A. saligna* effectively, it is crucial to have an understanding of *A. saligna's* seed dynamics and to determine its seed production and seed bank densities in the presence of biological control agents. This is needed to know the proportion of seed that will have to be actively

managed. Furthermore, the number of seeds produced within a season as well as the number of seeds that have accumulated over time is also an indication of the plants' growth rate under various environmental conditions. Therefore generating seed production and seed bank data over *A. saligna's* entire range in South Africa will indicate under which environmental conditions this invasive alien thrives and consequently where the largest amount of management resources will need to be invested to control and remove the plant. Lastly, knowledge of the seed bank dynamics will lead to an understanding of how to, as well as when to, implement management to successfully control *A. saligna*.

Term "seed bank dynamics" as used in the title and thesis

The term seed bank dynamics as used in the title and throughout the rest of this thesis refers to the fluctuation in size of the seed rain and seed bank of *A. saligna* over time as well as with different abiotic and biotic factors. Although the study was conducted over a short time-period through sampling the seed rain and seed bank of *A. saligna* populations of different age's, time was replaced with space giving an idea of how these parameters fluctuates through time.

Knowledge gap

A number of studies have estimated seed rain and seed bank size of *A. saligna*. However, the estimations of these studies were not representative of the whole distribution of *A. saligna*, especially for seed rain estimates (See Appendix C and D). Very little work has been conducted along the south coast from Cape Town towards Port Elizabeth. In addition, inland sites along the west and south coast are unrepresented in the previous studies. No information is available for *A. saligna* seed bank dynamics in the Eastern Cape. Furthermore an investigation of the effect of climate and soil conditions on the seed bank dynamics of *A. saligna* has been neglected. Therefore, there is a lack of information on the current seed bank and seed rain status of *A. saligna* over its whole distribution range in South Africa, including which environmental factors influence the variation of the seed bank dynamics. This study fills the gap by sampling over a wider area in the current distribution range of this invasive plant, providing a more complete picture of the variables driving seed production and seed bank accumulation. The study also serves as a revision on the work that has already been done. Ultimately it will further our understanding on seed bank dynamics, improving our capability to manage this invader effectively.

Study objectives

The primary study objective was to determine the seed rain and seed bank status of *Acacia saligna* across its distribution in South Africa. Secondly the study aimed to assess the influence of different abiotic and biotic factors on seed rain and seed bank size of *A. saligna*. This was done in order to predict under which conditions the seed rain and seed bank of *A. saligna,* as well as the plant in general, will be most problematic for control and management.

Study Framework

Chapter 1: is a literature review where I:

- Explain why it is of importance to take note of alien plants in South Africa and in the Western Cape.
- Define alien plants and the process by which species become aliens.
- Give a general background of the history of alien plants in South Africa.
- Highlight the importance of management and discuss various management options for alien plants.
- Review seed bank dynamics in general and that of Australian Acacias specificaly.
- Place *A. saligna* in context of all the discussed topics.

Chapter 2: deals with the seed production (seed rain) of *A. saligna* at different locations within its distribution range within South Africa. The effects of different abiotic and biotic factors on seed production are also explored.

Chapter 3: deals with the seed bank of *A. saligna* at different locations within its distribution range within South Africa. The effects of different abiotic and biotic factors on the seed bank are also explored.

Chapter 4: General conclusion.

Chapters 2 and 3 are written as stand-alone papers, and therefore there is some degree of necessary overlap between the two chaprers.

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Chapter 1: Literature Review

1.1. The Cape Floristic Region: location, importance and threats

The Cape Floristic Region (CFR) is situated in the Western Cape and stretches into the Eastern Cape of South Africa (latitudes 31° to 34° S) (Goldblatt, 1997). The CFR harbours one of six plant kingdoms globally (Van Wilgen *et al*., 1996) and has been selected as one of the world's significant areas for conservation action (Cowling and Heijnis, 2001; Cowling *et al*., 2003). This diverse floral region (Goldblatt and Manning, 2000; Goldblatt and Manning, 2002) only encompasses 90 000 km^2, smaller in extent than 4 % of the southern African subcontinent (Goldblatt, 1978). It is also one of five regions in the world characterised by a Mediterranean-type climate (Roura-Pascual *et al*., 2011).

The CFR holds approximately 9 030 indigenous vascular plants, about 8 920 being flowering plants, of which roughly 69 % are endemic (Goldblatt and Manning, 2002). The region's vegetation represents nearly 44 % of the 20 500 plant species of southern Africa (Goldblatt, 1997). The area's diversity and endemism is further enriched by a variety of mammals (Kerley *et al*., 2003), birds (Barnes, 1998), freshwater fish (Skelton, 1993; Skelton, 2001), amphibia (Minter *et al*., 2004), reptiles (Alexander and Marais, 2007) and invertebrates (Picker and Samways, 1996). The uniqueness and vulnerability of the CFR is recognised on a global scale as a biodiversity hotspot (Mittermeier *et al*., 1998; Myers *et al*., 2000), a Global 200 Ecoregion (Olson and Dinerstein, 1998), a Centre of Plant Diversity (Davis *et al*., 1994) and an Endemic Bird Area (Stattersfield *et al*., 1998).

Economically the CFR is also very important (Binns *et al*., 2001). The vegetation of the region is utilized for cut and dried flowers as well as for thatching grass (Binns *et al*., 2001). In 1993 it was estimated that these industries create 25 000 job opportunities and have an annual value of R80 000 million (Binns *et al*., 2001). Furthermore various fynbos species are used for food or medicinal purposes (Donaldson and Scott, 1994). Sadly, according to the Red list of South African plants, 1 803 (1 739 endemic) plant species in the CFR are estimated to be in danger of extinction and a further 3 219 (3 072 endemic) plant species are of conservation concern (Raimondo *et al*., 2009).

Invasive alien plants (IAPs) are a large threat to the unique vegetation of the CFR (Rebelo, 1992; Goldblatt and Manning, 2002), endowing numerous taxa with the status of being endangered or threatened (Van Wilgen *et al*., 1996; Raimondo *et al*., 2009). Furthermore, managers of natural areas in the CFR spend most of their time dealing with IAPs (Van Wilgen *et al*., 1992). The CFR

has been invaded by various trees and shrubs, particularly species of *Acacia*, *Eucalyptus*, *Hakea* and *Pinus* (Roura-Pascual *et al*., 2011). IAPs have the following negative impacts in the CFR; They:

- Replace natural vegetation (Van Wilgen *et al*., 1996; Holmes and Cowling, 1997a; Holmes and Cowling, 1997b; Vosse *et al*., 2008), transforming the landscape and reducing native species richness (Van Wilgen *et al*., 1994; Holmes and Cowling, 1997; Holmes, 2002; Latimer, 2004; Vosse *et al*., 2008).
- Reduce runoff from catchments in a water-scarce region (Van Wilgen *et al*., 1994; Roura-Pascual *et al*., 2011).
- Change fire regimes (Roura-Pascual *et al*., 2011) through altering vegetation structure and increasing fuel loads due to increased biomass (Van Wilgen *et al*., 1994; Van Wilgen *et al*., 1996).
- Alter soil chemistry (Witkowski, 1991a; Witkowski, 1991b; Musil, 1993; Stock *et al*., 1995; Yelenik *et al.,* 2004), transforming ecosystems and facilitating invasion by alien grasses (Richardson and Kluge, 2008).
- Lead to severe soil erosion through increasing fire intensities and reducing indigenous plant cover after fires (Scott and Van Wyk, 1990; Van Wilgen *et al*., 1996).
- Decrease aesthetic value of natural areas (Binns *et al*., 2001).
- Hamper management for example by complicating pre-scribed burning events (Van Wilgen *et al*., 1996).
- Provide cover for criminal activities (Milton, 1980).

1.2. Invasive alien plants (IAPs)

1.2.1. IAPs defined

IAPs can be defined simply as plant taxa that escape their native range, normally through anthropogenic activity, into a novel range where they persist, proliferate and spread (Richardson *et al*., 2000; Lockwood *et al*., 2007). IAPs may have significant negative impacts on the environment and based on these qualities are classified as transformer species (Richardson *et al*., 2000). Therefore, not all plant taxa introduced into areas beyond their geographical range are IAPs. Richardson *et al*., (2000) classified introduced plants species as follows:

- Alien plants: plant species existing in an area outside their native range due to deliberate or unintentional anthropogenic action.
- Casual alien plants: Alien plants that may flourish and even reproduce occasionally in an area, but do not form self-replacing populations, and rely on repeated introductions for their persistence.

- Naturalized plants: plants species that reproduce consistently and sustain populations over many life cycles without direct intervention by humans (or in spite of human intervention); they often recruit offspring freely, usually close to adult plants, and do not necessarily invade natural, semi-natural or human-made ecosystems.
- Invasive plants: Naturalized plants that produce reproductive offspring, often in very large numbers, at considerable distances from parent plants and thus have the potential to spread over a considerable area.
- Transformers: A subset of invasive plants which change the character, condition, form or nature of ecosystems over a substantial area relative to the ecosystems extent.

1.2.2. The invasion process

The invasion process consists of an introduction, naturalization and invasive phase (Sakai *et al*., 2001; Lockwood *et al*., 2007). Each stage requires species to overcome barriers limiting their spread (Richardson *et al*., 2000; Lockwood *et al*., 2007). The introduction phase requires species to overcome, through anthropogenic action, a major geographical barrier (Richardson *et al*., 2000; Lockwood *et al*., 2007). Furthermore, new populations must be initiated in the novel geographical range (Sakai *et al*., 2001). After species successfully pass the introduction phase they can be classified as alien plants. The naturalization phase requires alien species to overcome environmental and reproductive barriers (Richardson *et al*., 2000), and to establish a viable self-sustaining population (Sakai *et al*., 2001). Lastly, requirements for the invasive phase will have been met if a naturalized species is able to overcome dispersal barriers (Richardson *et al*., 2000). The ability of alien plants to overcome barriers will depend on propagule pressure, abiotic characteristics of the environment and biotic characteristics of the introduced plant and the native community (Lonsdale, 1999). Furthermore essential attributes impacting the successful spread of IAPs are the number of propagules, dispersal mode, and vital rates (birth and death) (Sakai *et al*., 2001).

1.2.3. Propagule Pressure

Propagule pressure can be defined as the total number of individuals released into an area (Williamson, 1996). Released individuals may be introduced on one or several occasions (Lockwood *et al*., 2005). Therefore propagule pressure can be divided into two components: number of introduction events and number of individuals per introduction event (Veltman *et al*., 1996; Lockwood *et al*., 2005). Increases in either one of these components will lead to an increase in propagule pressure (Lockwood *et al*., 2005). Propagule pressure is assessed to be significant in determining which areas are most vulnerable to invasion (Levine, 2000).

The total amount of time a species is present in an area also represents an attribute of propagule pressure (Becker *et al*., 2005; Hamilton *et al*., 2005). Time since introduction influences how invasion success is perceived, as newly introduced species may have small distribution ranges due to limited expanding opportunities (Gassó *et al*., 2009). As time passes, a species will have more propagule dispersal opportunities and the chance of establishing new populations will increase (Hamilton *et al*., 2005). Invasion history has been assessed as an effective predictor of invasiveness (Herron *et al*., 2007), as the invasion history will indicate number of seasons an alien species had to reproduce and establish.

The probability of an invader to be in a favourable environment is greater when propagule pressure is high, particularly with numerous introduction events (Catford *et al*., 2009). Frequent introductions may assist introduced populations to persist during unfavourable conditions (Lockwood *et al*., 2005) or when populations go through bottlenecks (Catford *et al*., 2009). High propagule pressure may lead to greater genetic diversity of introduced populations (Lockwood *et al*., 2005). This increases invasion risk through enhancing the probability of species adapting to ecosystem limiting conditions (Lockwood *et al*., 2005).

Seed saturation as a result of high propagule pressure, might lead to species establishment regardless of biotic and abiotic factors (Catford *et al*., 2009). Native plants, when competing with non-indigenous plants, tend to be more successful with adult-seedling competition than seedling-seedling competition (Crawley *et al*., 1999). Consequently, when native propagules overwhelm the seed pool, the chance they have to dominate alien species during colonization and establishment is greater (Catford *et al*., 2009).

Introduction frequency and number of propagules are greater in areas of low altitude (Becker *et al*., 2005). IAPs from low altitudes are more often used by horticulture (Van Kleunen *et al*., 2007). This results in higher frequency of introduction in novel environments as well as greater probability of naturalization outside their native range (Van Kleunen *et al*., 2007). Consequently, in low altitudes the greater diversity and abundance of IAPs may be ascribed to greater propagule pressure, the adaptation to low altitudinal conditions and intentional dispersal by humans (Gassó *et al*., 2009).

1.2.4. Abiotic factors influencing invasion

Establishment in novel environments requires alien species to cope with or adapt to prevailing environmental conditions (Wiether and Keddy, 1995; Catford *et al*., 2009). Invasive resistance of communities may lower if environmental conditions (abiotic or biotic) change, as alterations in environmental conditions will lead to changes in resource availability (Davis *et al*., 2000). Higher resource availability allows population growth, creates a chance for introduced species to colonize and may reset succession (Hood and Naiman, 2000). Resource release may occur at various

spatial and temporal scales and is normally a consequence of anthropogenic or natural disturbance (e.g. fire, herbivory, urbanisation etc.) (Sher and Hyatt, 1999; Davis *et al*., 2000). Alterations in the disturbance regime or frequency of disturbance may increase community vulnerability to invasion (Vitousek *et al*., 1996; Huston, 2004; Lake and Leishman, 2004). Therefore, the ability of an introduced population to become invasive may be encouraged by short-term increases in resources as well as long-term changes in disturbance regimes (Tickner *et al*., 2001) and environmental conditions in general (Williamson and Fitter, 1996).

1.2.5. Biotic Factors

1.2.5.1. Life history traits

Various life history traits of IAPs contribute to their success in habitats beyond their normal geographical distribution. Pioneer characteristics such as short juvenile periods, rapid growth, large propagule number and short intervals between cohorts, seem to be general indicators of successful colonists across taxa (Rejmánek and Richardson, 1996; Radford and Cousens, 2000; Kolar and Lodge, 2001; Richardson and Rejmánek, 2004; Hamilton *et al*., 2005; Herron *et al*., 2007; Gibson *et al*., 2011). Therefore invasive species performance is exceptional and native species are unable to compete with invaders in localities where resources are readily available (Daelher, 2003). Other attributes also shown to facilitate invasion are: vegetative reproduction, perfect flowers, seed lacking a need for a pre-germination treatment (Reichard and Hamilton, 1997), large natural latitudinal range and plastic growth form (Herron *et al*., 2007) and long flowering period (Goodwin *et al*., 1999).

1.2.5.2. Community vulnerability

Communities vary in their vulnerability to invasion (Usher, 1988; Sakai *et al*., 2001) and few are completely invasion resistant (Gordon, 1998; Sakai *et al*., 2001). Successful invasion within communities is a consequence of invasive species, native species and community characteristics (Sakai *et al*., 2001). Invasion may be due to species having similar or different attributes as indigenous species, with dissimilar traits allowing the occupation of vacant niches (Sakai *et al*., 2001). Furthermore, the larger the area of introduction, the greater the probability of successful establishment and invasion, as the variety of habitat types in which the introduction occurs will be higher and therefore the likelihood of establishing in a susceptible one is high (Radford and Cousens, 2000).

1.2.5.3. Native species richness and interactions

Native species interactions may negatively impact alien species number and spatial distribution. Consequently, the establishment of alien species in native communities may be prevented (Sakai *et al*., 2001). Indigenous plant species are adapted to the local environment, and should competitively exclude alien species which evolved under different environmental conditions (Moles *et al*., 2008). Resource availability influences competition, subsequently affecting invasion (Davis *et al*., 2000; Sakai *et al*., 2001). As discussed previously, events such as disturbance, herbivory and pest outbreaks increase available resources thereby increasing invasion probability (Davis *et al*., 2000).

IAPs are often successful as a consequence of a decline in interspecific interactions (Sakai *et al*., 2001). The lack of enemies for alien species in their introduced environment may lead to rapid population growth (Blossey and Nötzold, 1995; Keane and Crawley, 2002). In the absence of these biological constraints more resources could be available for invasive species leading to their greater competitive ability (e.g. faster vegetative growth) and ability to invade (Blossey and Nötzold, 1995; Mack *et al*., 2000). Mutualisms may help alien species to become invasive or mutualisms may aid community resistance (Richardson *et al*., 2000). In conclusion it should be noted that the probability of a community to be invaded is a characteristic that fluctuates over time (Davis *et al*., 2000).

1.3. History of IAPs in South Africa

Exotic species in South Africa have been introduced from Australia, Asia, Europe, elsewhere in Africa, South America and North America. Most of these species, including the worst weeds, are native to Australia and South America. The success of Australian and South American species may be ascribed to a pre-adaptation to South Africa's ecological conditions. Nearly all of the first non-native introductions were made in Cape Town or the south-western Cape (Shaugnessy *et al*., 1978).

The release of exotic species into South Africa is a consequence of the first settlers needs for edible plants and to introduce something of their 'home environment'. Their lack of knowledge of indigenous flora may further have promoted the importation and use of alien plants. Even with the introduction in 1652 of exotic species characteristic of European gardens at that time, only two species, *Pinus pinaster* and *Opuntia ficus-indica* were recognized as serious invasive plants by 1810. Consequently most of the worst weeds were introduced afterwards (Shaugnessy *et al*., 1978).

The 19th century saw great interest in the growing of alien plants, especially for botanical gardens. Three botanical gardens were established during the first half of the 19th century. Two in Cape Town, the C F H von Ludwigs Garden and the Cape Town Botanical Garden, and one in the Eastern Cape, the Grahamstown Botanical Garden. The gardens not only assisted introductions of alien species but also promoted their dispersal through distributing seed and material to interested individuals. Amongst the numerous plants collected for these institutions were various species, including species from Australia, which later became recognised as IAPs (Shaugnessy *et al*., 1978).

During the 1840s and 1850s the sand dunes of the Cape flats had to be stabilised to maintain the newly constructed road that ran from Cape Town through Bellville. An experimental programme was initiated planting both native and exotic shrubs and trees. A similar project was established in the Eastern Cape to stabilise a location of windblown dunes. This area stretched across Cape Recife Point from “the Gulchways” to the harbour of Port Elizabeth. The species used for sand dune stabilisation included, among other several Australian acacia species, pine species and exotic grass species (Shaugnessy *et al*., 1978).

After 1875 timber plantations, mainly of cluster pine, were planted in Cape Town. Different exotic trees were planted between the pines, as hedges and as fire breaks to protect the pine trees at different stages of their development against the elements and animals. Cluster pines, Australian *Acacia* and *Hakea* are still present in these areas and remain as proof of these plantations (Shaugnessy *et al*., 1978).

Land owners found the easily propagated and fast growing exotics very desirable in a region where large trees are mainly absent. The trees could be used for many useful purposes including: hedges, wind-breaks, tanning, fire wood and timber. Consequently, it is of no surprise that exotic species were so readily used. The broad distribution of various species in the Cape now considered to be IAPs is a result of deliberate planting. These species were also chosen for their adaptation to a Mediterranean climate and their ability to grow fast. As a consequence in the CFR they were able to establish and become naturalised and in some cases even become invasive (Shaugnessy *et al*., 1978).

1.4. Management of IAPs

Globally environmental managers acknowledge the need for effective control programs to combat impacts of IAPs. Consequently numerous efforts have been made to establish such programmes, some successful and others complete failures. However, even failures can be valuable if they are documented and used to guide future management (Van Wilgen *et al*., 2001).

Even with a sound understanding of a species biology and ecology, the implementation of integrated control measures might still prove difficult. Furthermore unexpected disturbances, such as fire and floods, uncertainties around budgets and funding as well as unpredictable outcomes of management efforts can further complicate matters. Consequently management becomes a practise of trial and error, leading to great expenses which can be ill afforded (Van Wilgen *et al*., 2001). There is a need to develop practical guidelines for management that incorporates past experience to at least prevent the same mistakes being made elsewhere (Van Wilgen *et al*., 2001; Wilson *et al*., 2011).

To effectively manage IAPs, efforts of managers and the public in general need to focus on the different stages of the invasion process (Van Wilgen *et al*., 2001). As previously mentioned, the invasive process consists of an introduction, naturalization and invasive phase (Sakai *et al*., 2001; Lockwood *et al*., 2007). It is during the invasive phase that integrated control programs find a logical place. Prevention, early detection and removal are more applicable to the first two stages; such practises usually include risk assessment frameworks, cost-benefit analysis and continual monitoring. When a species becomes invasive, management options may be very limited (Van Wilgen *et al*., 2001; Wilson *et al*., 2011). Generally there are five stages during a plants' life cycle to which control measures can be applied: seedling establishment, sapling or adult growth, flowering and seed production, seed dispersal and seed bank establishment (Wilson *et al*., 2011). In order to sustainably manage alien plants, mechanical, chemical, cultural and biological control options need to be applied in combination at the different life cycle stages (Van Wilgen *et al*., 2001; Richardson and Kluge, 2008; Wilson *et al*., 2011).

1.4.1. Chemical Control

Most plant invaders can be killed by one or other herbicide (Stirton, 1978). Herbicides have proven useful in preventing the coppicing of plants and to destroy seedlings germinating after felling or burning. Chemicals can be used to kill specific plants leaving other species unharmed. However, even with chemicals being improved to be less toxic and to have shorter residence times, there are still concerns over negative environmental impacts (Van Wilgen *et al*., 2001). In South Africa herbicide application is strictly regulated (Stirton *et al*., 1978). Before chemicals can be used against specific plants or plant groups they have to be tested and registered (Stirton *et al*., 1978). In addition, the application of chemicals needs high levels of training. These factors, in combination, limit the use of herbicides on a large scale (Van Wilgen *et al*., 2001).

1.4.2. Mechanical Control

Mechanical control consists of slashing, felling, frilling or ring-barking plants and includes cultural practices for instance burning, ploughing and afforestation (Stirton *et al*., 1978; Van Wilgen *et al*., 2001). The implementation of such activities require the use of saws, scythes, picks, hoes, ploughs, mowers, long-handled clippers, chains, chainsaws and bulldozers (Stirton *et al*., 1978; Van Wilgen *et al*., 2001). Physically removing invasive alien plants is labour-intensive and consequently costly in dense infestation or in remote or rugged locations (Van Wilgen *et al*., 2001). Stirton *et al*., (1978) indicated the following techniques for use on different plant invaders:

- Handpulling with stout gloves
- Grubbing, hoeing and digging out
- Ring-barking
- Cutting the stem as near as possible to the ground and peeling off bark into the ground
- Slashing or crushing, with chemical application
- Sawing, without chemical application to the stump
- Sawing with chemical application to the stump
- Ploughing
- Chain-pulling, using tractors to pull plants into windrows or piles
- Burning
- Afforestation
- Removal from water to an area where they will desiccate and die.

1.4.3. Biological Control

The success of many invasive plants in South Africa may be a consequence of the lack of natural enemies (Stirton *et al*., 1978). In their native range their vigorous growth and mass seed producing capability is regulated by a host of co-evolved species (Van Wilgen *et al*., 2001). Therefore it may be possible in time to decrease the aggressiveness of invasive plants through introducing some of their natural enemies from their native range as biological control agents (Stirton *et al*., 1978; Van Wilgen *et al*., 2001). Regularly, however, the natural enemies of weeds in their native environment cannot be released in the area where they have become invasive. This might be because they are unable to establish in the new environment or because they are not host specific and attack native or commercially used species. It is of great importance that biological control agents are properly screened before they are released into a country but this process may be tedious and time consuming (Stirton *et al*., 1978). If biological control is implemented correctly there are many potential benefits for example reduction in management expenses (Van Wilgen *et al*., 2001).

1.4.4. The largest obstacle

There is one particular life stage preventing the effective and sustainable removal of IAPs (Richardson and Kluge, 2008; Wilson *et al*., 2011). This is the ability of various alien plant species to accumulate and maintain a persistent seed bank (Milton and Hall, 1981; Esler and Boucher, 2004; Richardson and Kluge, 2008; Wilson *et al*., 2011). Methods focusing on the destruction of mature plants are highly unlikely to effectively remove species investing in a soil stored seed bank (Richardson and Kluge, 2008). These removal techniques will only stem the problem in the short-term (Richardson and Kluge, 2008).

1.5. Seed bank dynamics

The soil seed bank consists of all seed, capable of germinating, on top or below the soil surface or in the associated litter (Simpson *et al*., 1989). The seed bank in an area may consist of propagules produced in the vicinity or from other localities (Harper, 1977). As seed is continually added to the seed bank it represents both past and present plant communities (Harper, 1977). Seed present in the seed bank have spatial and temporal dimensions (Simpson *et al*., 1989). Dispersal from the parent plant onto the soil and movement of seed thereafter, result in seed having both a horizontal and a vertical distribution (Simpson *et al*., 1989). Usually seed reach the earth's surface in a dormant state (Harper, 1977). Propagules may require specific germination queues in order to break dormancy (Harper, 1977). Environmental conditions experienced by seed on the soil surface may further impose dormancy (Harper, 1977). Consequently seed banks can be either transient, with seed persisting in the soil for less than a year, or persistent, with seed lasting in the soil for a period greater than one year depending on their germination requirements (Simpson *et al*., 1989; Fenner and Thompson, 2006). The latter can further be divided into short-term (<5 years) and long-term (>5 years) persistent seed banks (Fenner and Thompson, 2006).

The potential population of an area is determined by the increase and decrease of propagules (Harper, 1977). Seed bank input is a consequence of seed rain (Fig. 1.1) (Harper, 1977; Simpson *et al*., 1989). Input can either be from local or outlying seed sources (Harper, 1977; Simpson *et al*., 1989). Dispersal may occur through passive means for example mechanical ejection of seed or through fire, wind, water and animals (Simpson *et al*., 1989; Fenner and Thompson, 2006). This flow of propagules into and out of an area forms an integral part of plant population dynamics (Harper, 1977).

Seed bank losses result from seed germination, deep burial or re-dispersal, decay, predation, fire, pathogens, failed germination and physiological death (Fig. 1.1) (Harper, 1977; Simpson *et al*., 1989; Esler and Boucher, 2004). Seed density, species composition and genetic reserve are results of seed gain and losses, with other life history processes indirectly impacting these

parameters (Simpson *et al.*, 1989). Seed bank dynamics are regulated by changes in the relative significance of these processes over time (Simpson *et al.*, 1989).

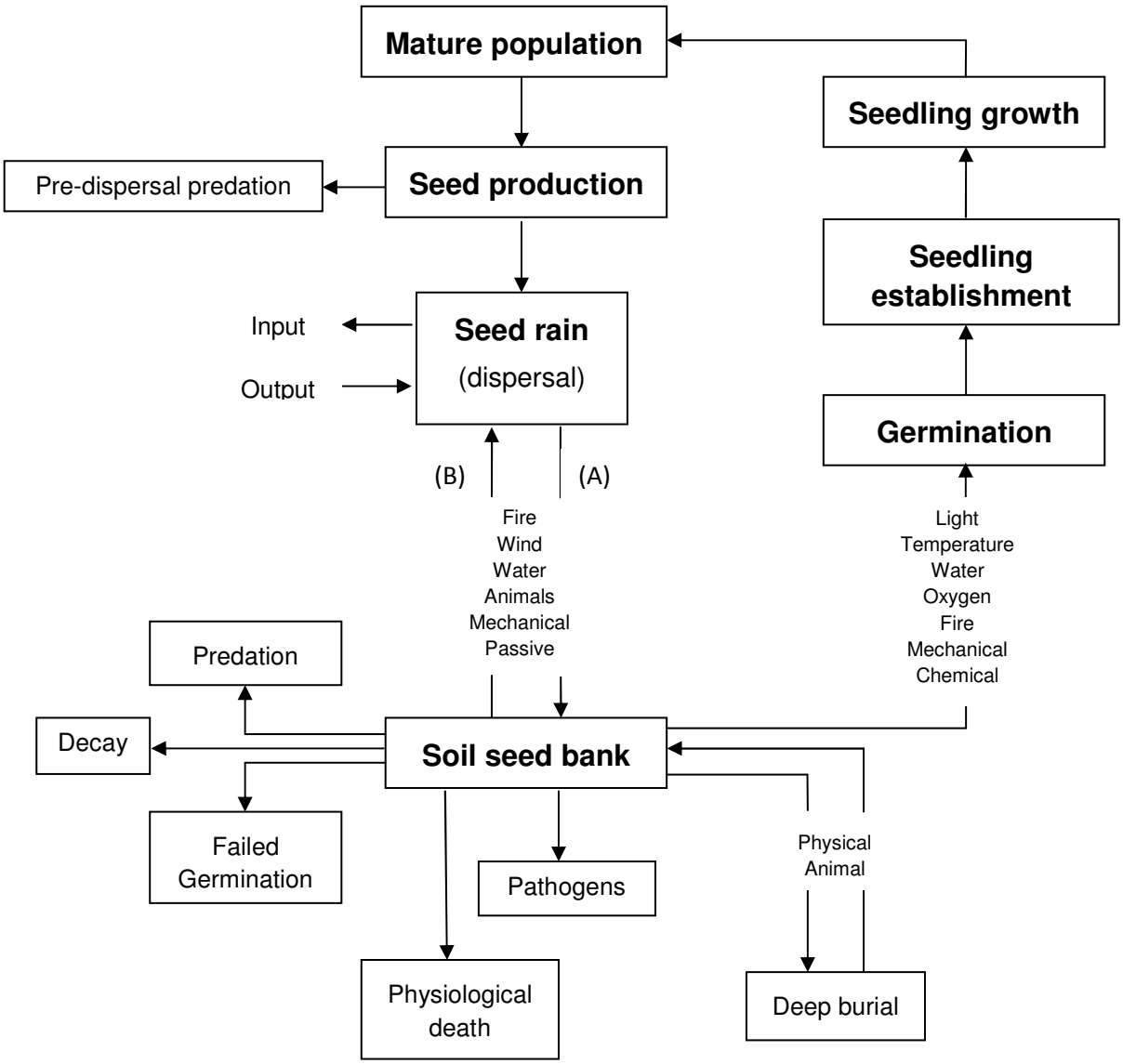

Figure 1.1: Simplistic model illustrating seed bank dynamics. Adapted from Simpson *et al.*, (1989) and Pieterse (1997). (A) indicates primary dispersal; (B) indicates secondary dispersal.

Seed banks guard plants against environmental heterogeneity (Venable and Brown, 1988). The greater the risk of loss of all offspring during any one reproductive season, the stronger the selection for a seed bank should be (Cohen, 1966). Draw backs of seed banks are higher probability of seed mortality and extended time periods before reproductive efforts are realised by seed germinating and establishing (Fenner and Thompson, 2006). Possessing a seed bank has the greatest benefits when heterogeneity is mainly temporal (McPeek and Kalisz, 1998). Consequently seed banks should have the greatest benefits in environments where disturbances are regular and devastating, but relatively erratic (Fenner, 1985; Fenner and Thompson, 2006). In contrast seed banks will be of little significance in stable environments (Fenner, 1985; Fenner and

Thompson, 2006). Persistent seed is more a consequence of disturbance irregularity than severity (Fenner and Thompson, 2006).

1.5.1. Dispersal and spatial distribution

Dispersal enables established populations to persist in ever changing population mosaics and allow populations to increase their range and size outside their current distribution. The importance of dispersal in the survival of plant populations is a consequence of the spatial and temporal heterogeneity of their environment. The present distribution and population size of a species is in part a consequence of its current dispersal mechanisms (Harper, 1977). Harper (1977) stated that small population size may be a consequence of the following:

- Areas suitable for establishment are few;
- Suitable areas are separated by distances far greater than the dispersal ability of the species;
- Suitable areas have low carrying capacities;
- The time during which new suitable sites are available are short relative to the dispersal rate of propagules;
- The suitability of an area remains so for only short periods of time;
- Colonization and full exploitation of the carrying capacity of a habitable site is slow.

The spatial distribution of a population's seed bank could be crucial for establishment as habitats vary spatially (Parker *et al*., 1989). Source individuals mainly determine spatial distribution patterns and consequently the environment in which seedlings will have to establish (Leck, 1989). The movement of seed from their point of origin to the earths' surface is influenced by various factors (Harper, 1977). The height and distance of the origin point, seed crop size, timing of seed release, dispersibility of seed (weight, plumes etc.), distributing agent activity (wind direction and velocity, density of animal dispersers etc.) and fluctuations in environmental conditions such as differences in soil texture all play a role during dispersal (Harper, 1977; Bigwood and Inouye, 1988; Leck, 1989; Willson and Traveset, 2000). Most seed are usually found near the parent plant with a decrease in seed density with distance from it (Harper, 1977; Milton and Hall, 1981; Parker *et al*., 1989; Auld, 1996; Willson and Traveset, 2000). However, other abiotic and biotic factors may lead to variation in spite of an initial homogenous post-dispersal distribution of seed (Parker *et al*., 1989).

Seed on the soil surface do not necessarily remain stationary (Harper, 1977; Bigwood and Inouye, 1988). They may be moved along the surface by wind or water (Harper, 1997; Milton and Hall, 1981; Bigwood and Inouye, 1988; Richardson *et al*., 1992) until they are caught by obstacles or fall

down crevices (Harper, 1977; Bigwood and Inouye, 1988). Certain species have developed seed with special mechanisms enabling them to move horizontally or to bury themselves (Harper, 1977).

The loss of seed due to predation and other associated predator behaviour could be of significant importance in reducing the number of seedlings that will successfully establish in the future (Milton and Hall, 1981; Garwood, 1989; Parker and Kelly, 1989; Holmes *et al*., 1987). The impact of predation may be considerable and differential (Parker *et al*., 1989; Holmes, 1990a), depending on predation intensity (Louda, 1989). Furthermore seed may be dispersed by animals (Milton and Hall, 1981; Bigwood and Inouye, 1988; Holmes, 1990a; Holmes 1990b; Auld, 1996) influencing their distribution pattern in complex ways for example through their often very specific feeding habits and territorial and migratory behaviour (Harper, 1977). Dispersal may also be enhanced by seed moving through the digestive tract of animals (Harper, 1977; Glyphis *et al*., 1981; Auld, 1996). Seed may be passively distributed by animals with their movement and grooming behaviour determining the place of deposition (Harper, 1977; Bigwood and Inouye, 1988; Auld, 1996). Animals might also actively gather and hoard seed, storing them in localized aggregations (Harper, 1977).

Human activity has lead to the widespread dispersal of seed within their native ranges as well as over continental barriers. Within native ranges of species humans might even create focal points for the establishment and development of plant populations. This is particularly so in areas developed for agricultural use. After these initial dispersal processes seed are further dispersed into the soil (Harper, 1977).

1.5.2. Incorporation of seed into the soil

The largest number of seed is situated near the soil surface and declines markedly with depth (Harper, 1977; Hill and Stevens, 1981; Milton and Hall, 1981; Pickett and McDonell, 1989; Tozer, 1998; Holmes, 2002; Strydom *et al*., 2012). Many seed may be present in the litter which will lead to constant addition to the number of seed in the soil (Hill and Stevens, 1981). There are fewer seed in the humus and litter layer than in the soil (Hill and Stevens, 1981). In some environmental situations, for instance fire prone habitats, the distribution of seed within the soil is crucial for survival (Parker and Kelly, 1989). Under these conditions soil temperatures could lead to the destruction of seed near the soil surface, the germination of seed below that, and could be of no consequence to seed very deep in the soil profile (Parker *et al*., 1989).

Little is known about the processes by which seeds are incorporated into the soil (Garwood, 1989; McGraw and Vavrek, 1989; Leck, 1989; Holmes, 1990c). However, this is fundamental in uncovering vertical and horizontal spatial patterns and determining longevity of seed banks (Garwood, 1989). Water eroded soil could bury seed in situations where the water is not frozen

(Cavers and Benoit, 1989). Rain may wash small seed into coarse textured soil (Hopkins and Graham, 1983; Bigwood and Inouye, 1988; Benvenuti, 2007). Movement of seed in the soil profile may be attributed to percolation, with small seed moving faster than larger seed (Harper, 1977; McGraw, 1987; Bigwood and Inouye, 1988). Less seed persist in soil that is frequently water saturated (Leck, 1989). Furthermore, cracks in the soil could be formed through freezing and thawing cycles into which seed could be moved by melted snow or rain. Similarly, earthworm burrows, openings in the soil left after root decay and cracks formed after very dry periods, could allow seed to move into the soil (Harper, 1977; Bigwood and Inouye, 1988; Cavers and Benoit, 1989). Coarser texture may allow faster passive movement of seed into the soil (Benvenuti, 2007).

Some seed have self-burial mechanisms which facilitate their incorporation into the soil (Harper, 1977). The build up of leaf litter on the soil after seed fall may lead to the burial of seed (Harper, 1977). The incorporation of seed into the soil could also be assisted by earthworms, burrowing mammals, and other animals (Harper, 1977; Milton and Hall, 1981; Holmes, 2002). Some animals for example scatter-hoarding rodents (Garwood, 1989), ants (Roberts and Heithaus, 1986; Holmes, 1990a; Holmes, 1990b; Midgley and Bond, 1995; Auld, 1996; Tozer, 1998; French and Major, 2001) and earthworms (Harper, 1977) also actively bury seed in the soil. Furthermore larger terrestrial animals could also assist seed burial through digging holes (Young, 1985).

Seed occurring deep in the soil profile are usually small (Harper, 1977) and buoyant seed are usually found near the soil surface (Leck, 1989). The rate and depth of seed burial is also influenced by sedimentation and soil compression (Leck, 1989). The position of seed in the soil profile determine if seed will be exposed to conditions required for germination, as well as whether the shoot will reach the surface after germination (Leck, 1989). The processes described above are spatially heterogeneous (Garwood *et al*., 1989). Consequently, the distribution of seed in the soil should vary tremendously over short distances (Garwood *et al*., 1989).

1.5.3. Loss of seed in the soil

The density of viable seed situated in the soil, decreases continuously as a result of germination and rotting (Milton and Hall, 1981; Cavers and Benoit, 1989; Parker *et al*., 1989; Holmes *et al*., 1987; Holmes, 1989; Auld, 1996). Differential seed bank decay patterns may arise as a consequence of different environmental factors fluctuating within an area (Baker, 1989; Baskin and Baskin, 1989). The decline in the seed bank as a consequence of germination is largely confined to the upper soil layer (Cavers and Benoit, 1989; Homes and Moll, 1990; Tozer, 1998; Grundy *et al*., 2003; Esler and Boucher, 2004) and is strongly tied with spatial variation in microclimate (Parker *et al*., 1989). For instance, seed of ruderal species in forests are very sensitive to changes in light levels (Garwood, *et al*., 1989). In recently disturbed locations, the seed bank of such ruderal

species are small and gain size with distance from the disturbed area into the forest (Parker *et al*., 1989).

The size and shape of the seed as well as its orientation on or within the soil will determine the contact the seed make with the substrate. This will influence the ability of the seed to absorb water and consequently whether the propagule will germinate successfully. Seed residing on the soil surface will lose water to the atmosphere. Therefore the contact between the seed and the substrate surface must be sufficient enough to allow the propagule to absorb water faster than it is lost to the atmosphere. Large seed loose water faster to the atmosphere than smaller seed. Humidity will influence the rate seed loose water to the atmosphere. The greater the humidity the slower water loss will be. Therefore the microtopography of an area greatly influences germination, as subtleties in the microsites on the various surfaces provide different opportunities for germination (Harper, 1977).

While seed underneath leaf litter or in the soil are protected against fast water loss to the atmosphere additional energy is required to extend its photosynthetic surface above the leaf litter or soil surface. Larger seed are able to germinate from further down the soil profile than smaller seed as their energy stores are greater. Soil compaction also affects the probability of seed in the soil producing an emerged seedling. When soil compaction is high the chance of a germinating seedling penetrating this physical obstacle is low. A group of seedlings have a greater chance of breaking through such a layer (Harper, 1977).

While a seed is germinating it uses little of the available resources in its immediate environment other than oxygen and water. Most seed contain an adequate store of nutrients to fuel the development of the seed into a seedling well beyond the point where it can begin to photosynthesize (Haper, 1977).

Soil-water content, aeration and penetrability are affected by soil texture through the relationship between particle size and interparticle pore space. Soil water content is a function of the pore size and also of the water tension within the soil. Soil absorbing water and soil loosing water will have different water contents at the same tension. Consequently pore size influence germination as it will determine the quantity of water available for germination and seedling establishment (Harper, 1977).

Pathogens attacking the propagule as well as the infection severity greatly affect its viability (Pitty *et al*., 1987). Associated with pathogenic damage are the alterations in the seed due to biological or mechanical wounding (Cavers and Benoit, 1989). For example wounding may lead to germination through overcoming primary dormancy (Foley, 1987).

Only a small number of the many seed residing in the soil and on its surface germinate and become seedlings. Seedlings will be present wherever the environment is suitable for germination

of seed and their subsequent development. The suitability of areas for germination are not only a result of the elements they provide for seedling establishment but also as they exclude processes leading to their death such as predators, competitors, toxic soil compounds and pre-emergence pathogens . A species may not be in an area either because there are no suitable sites available even if a large number of its seed are present in the soil or suitable sites are available but have no seed. Seedling density may vary as a consequence of varying seed densities dispersed into a uniformly suitable environment or varying availability of suitable locations when seed are abundant. The successful establishment of a seedling depends on the suitability of its immediate environment and the successful establishment of a population of seedlings rely on every individual residing in such an environment (Harper, 1977).

The seed of species differ in their longevity and long lived seed are usually annuals or biennials, small in size and characteristic of disturbed areas (Harper, 1977). Legumes are an exception with many woody species having long persistent seed banks. Seed of the same species may vary greatly in their longevity. These differences are mainly a consequence of variation in dormancy resulting from intricate interactions of genetic and environmental factors (Cavers and Benoit, 1989). Factors impacting longevity take place during the production of seed, after dispersal or before and after seed are incorporated into the soil (Cavers and Benoit, 1989). Viability may decline only as a consequence of age (Harper, 1977). In the absence of pathogens and other seed damaging organisms, seed viability decrease as mutations build up during dormancy, and irreversible biochemical changes occur which lead to death (Harper, 1977).

1.5.4. Effect of soil properties on seed banks

Soil type can influence seed bank composition and density (Cavers and Benoit, 1989; Pickett and McDonell, 1989). In some circumstances soil characterized by low pH will support smaller seed banks as the above ground vegetation may produce less seed or more seeds may germinate under these conditions (Brown and Oosterhuis, 1981). The presence of small seed banks in peat soils can be a consequence of poor permeability of such soils to seed (Hill and Stevens, 1981). Substrate chemistry could also have an impact on the size and composition of seed banks (Leck, 1989). Germination of some species persisting in the soil may be limited as a result of soil salinity (Leck, 1989).

Seed bank size and nature is greatly affected by soil moisture content (Cavers and Benoit, 1989). Seed germinate more rapidly in well-drained sandy soil, regardless of depth, than in medium or poorly drained clay loams (Cavers and Benoit, 1989). Consequently in sandy soil the seed bank is exhausted faster (Cavers and Benoit, 1989). Similarly soils that are more moisture saturated have

less seed germinating and therefore contains a more persisting seed bank (Pareja and Staniforth, 1985).

Dry soils have larger daily fluctuation in temperature than moisture saturated soils (Daubenmire, 1974). Therefore, very wet soils sustain dormancy and viability in seed requiring daily temperature fluctuations to germinate (Cavers and Benoit, 1989). In contrast very dry soils maintain dormant and viable seed until enough moisture is present for germination (Cavers and Benoit, 1989). Other soil properties impacting the size and composition of seed banks include percentage plant cover, soil density, soil aeration, and the occurrence of volatile germination inhibitors or allelochemicals (Cavers and Benoit, 1989).

1.5.5. Persistent seed banks

As stated above persistent seed banks consist primarily of small sized, light weight seed, particularly of weedy and ephemeral species (Harper *et al*., 1970; Fenner, 1985). Chemical defences (Janzen, 1969) and specialised dispersal mechanisms are not normally attributes of seed persisting in the seed bank (Harper *et al*., 1977). Dormancy mechanisms in contrast are rather the norm than the exception in persistent seed (Baskin and Baskin, 1989). There are species that produce individual seed which display tremendous potential longevity, but their role in population dynamics seem irrelevant (Louda, 1989). However, the age and genetic structure of seed in the soil is a consequence of dormancy (Louda, 1989). This structure usually absorbs the effect of disturbance on population dynamics in the short-term through spreading risk and diminishing the impact of irregular fluctuations (Harper 1977; Louda, 1989).

Only some plant species within a community occur in the persistent seed bank over time (Louda, 1989). Persistent seed banks usually consist of: (i) pioneer and ephemeral species (Harper, 1977) or (ii) the ever-present monospecific dominant plant (Silvertown, 1982). Pioneer species are only present for a short period, particularly annual weeds growing early in succession (Louda, 1989). The ephemerals are mainly annuals of environments that are unforgiving or episodic (Louda, 1989).

Long-term seed banks form an evolutionary-memory guarding against rapid adaptation in response to environmental fluctuations (Brown and Venable, 1986). The effect of a single years drift, as a consequence of an extreme change in conditions, will be smaller as the dormancy of seed increase (Parker and Kelly, 1989). In fire adapted systems, postfire germination *en masse* lead to the absence of a regenerative guard against local extinction for annuals or obligate-seeding shrubs or to strong environmental selection during seedling establishment (Parker and Kelly, 1989). This population behaviour is more characteristic of annuals without seed dormancy (Parker and Kelly, 1989).

The size of persistent seed banks varies significantly; even in a given vegetation type (Parker *et al*., 1989). The rate of accumulation is to some extent a consequence of the portion of each year's seed input remaining dormant (Parker *et al*., 1989). Seed longevity is also essential; the greater seed longevity the faster a persistent seed bank will accumulate (Parker *et al*., 1989).

As the vegetation in a location moves through different stages of succession there are significant changes in the environment at and beneath the earth's surface which modifies its suitability for a seed bed. For instance as the canopy develops there is a increase in shading which in turn change the light intensity and quality at the soil surface, alters direct evaporation from the surface and lead to the formation of a area generally higher in humidity and more equable in temperature. Furthermore the accumulation of litter and their decomposition alters the physical and chemical characteristics of the soil and may lead to the burial of seed lying on the soil surface. The state in which the environment resides is changed by these developments. Consequently its suitability for the germination of seed is also altered (Harper, 1977).

1.6. Australian Acacias

Approximately 1012 species of *Acacia* are native to Australia (Richardson *et al*., 2011). About 70 species of Australian *Acacia* has been introduced to South Africa (Richardson *et al*., 2011) over the last 200 years (Shaugnessy *et al*., 1978), of which 14 have become invasive (Richardson *et al*., 2011). *Acacia mearnsii*, *A. saligna*, *A. cyclops* and *A. dealbata* are in the top ten of the fifty most problematic and widely distributed IAP species in South Africa (Henderson, 2007).

In South Africa, less than 1 % of the flowers formed by *A. cyclops, A. longifolia, A. podalyriifolia, A. saligna* and *A. melanoxylon* produce mature pods (Milton and Hall, 1981). There are no records of native species targeting the flower buds and flowers of Australian Acacias (Richardson and Kluge, 2008). *A. saligna* produces the most seed of all the Australian Acacias in South Africa (Gibson *et al*., 2011) and has an estimated annual seed rain ranging from 460 seed m^{-2} to 13 472 m^{-2} (Wood and Morris, 2007). It has been determined that 2 year old *A. saligna* saplings are able to produce seed (Milton and Hall, 1981). However, *Acacia* only produce large quantities of seed from age 5 (Milton and Hall, 1981). Milton (1980) estimated that on average only 2.3 % of freshly fallen seed of *A. cyclops, A. longifolia, A. podalyriifolia, A. saligna* and *A. melanoxylon* are able to germinate immediately. The remaining seed are added to the permanent seed bank were they persist until the testa is sufficiently ruptured to allow the absorption of water and consequent germination (Milton and Hall, 1981). Some of the Australian Acacias are bird dispersed, for example *A. cyclops* and *A. melanoxylon.* The seed of ornithochorous species are temporarily vulnerable in the canopy to predation by birds while being presented for dispersal (Glyphis *et al*., 1981; Richardson and Kluge, 2008). Seed that moved through the digestive tract of birds are

scarified removing their physically imposed dormancy (Glyphis *et al*., 1981) and will germinate more readily (Richardson and Kluge, 2008). It has been reported that native alydids attack and markedly damage seed of *A. cyclops (*Milton and Hall, 1981*), A. melanoxylon* and *A. implexa* (Pieterse, 1998). However, the impact of the alydids was in the past not high and consistent enough to stop the species from establishing and spreading (Richardson and Kluge, 2008).

Seed in the litter layer is vulnerable to fire, predation by rodents, insects and birds and may also rot (Richardson and Kluge, 2008). Holmes (1990b) estimated a loss of 50 % and 80 - 90 % of the annual seed input in the litter layer of *A. saligna* and *A. cyclops* respectively due to predation, rotting and burial by ants. Seed of *A. saligna, A. longifolia* and *A. mearnsii* have eliaosomes which attracts indigenous ants which will then bury them (Midgley and Bond, 1995; French and Major, 2001). Ants bury seed in their nests at depths of 4 - 7 cm (Bond and Slingsby, 1983; 1984), consequently incorporating them in the soil seed bank and making them less vulnerable to fire (Richardson and Kluge, 2008). The bird dispersed seed of *A. cyclops* are also buried by ants but to a lesser extent (Holmes, 1990b). In South Africa ants may play an integral part in the incorporation of Australian *Acacia* seed in the soil seed bank (Holmes, 1990b). The vertical movement of seed not buried by ants are slow and was estimated to be 3 % after 1 year in sand plain fynbos (Holmes, 1990c). Rodents, mainly the striped field mouse (*Rhabdomys pumilo*) are slower to take seed of Australian Acacias than ants (Holmes, 1990b) and it is estimated that they only remove 1 % of the annual seed production (Milton and Hall, 1991).

Seed bank densities of Australian Acacias in the soil have been measured to be between 1 430 m^{-2} for *A. cyclops* (Holmes *et al.,* 1987) and 212 000 m^{-2} for *A. saligna* (Morris, 1997). The largest proportion of the seed bank in the soil is situated in the top 10 cm (Milton and Hall, 1981; Strydom *et al*., 2012). Most of Australian *Acacia* seed situated in the soil are viable (85 %) (Milton and Hall, 1981) and are able to remain so for 50 years or more (Holmes, 1989). The proportion of Australian *Acacia* seed in the soil that are unable to germinate is low: *A. cyclops* (5.2 %), *A. longifolia* (1.5 %), *A. melanoxylon* (0 %) and *A. saligna* (1.0 %) (Milton and Hall, 1981). Pieterse and Boucher (1997) found older *A. mearnsii* seed to be just as viable as younger seed but to display less vigour when germinating. Approximately 90 % of seed in the soil seed bank will not germinate as a result of physical imposed dormancy (Richardson and Kluge, 2008). Previous studies have determined seed dormancy levels of 90.8 – 91.2 % for *A. saligna* and 89.6 – 93.4 % for *A. cyclops* (Milton and Hall, 1981; Holmes, 1988). However, the majority of *A. cyclops* seed germinate within 1 year after passing through the digestive tract of birds (Richardson and Kluge, 2008). Seed of *A. cyclops* close to the soil surface germinated more tardily than seed deeper in the soil profile that are assessed to be older (Milton and Hall, 1981). Pieterse and Cairns (1986) found 3.7 % and 0.01 % of *A. longifolia* seed to germinate in burnt and unburnt plots respectively. The seed of Australian *Acacia* in the soil stored seed bank show no difference in viability and dormancy when compared to fresh material (Milton and Hall, 1981).

Seed situated in the soil below a depth of 10 cm have a smaller probability of germinating (Holmes and Moll, 1990). However, germination of seed from a soil depth of 15 cm has been recorded (Holmes and Moll, 1990). Seed occurring at these depths are better insulated from temperature fluctuations at the soil surface (Richardson and Kluge, 2008). Therefore, these seed will have physical dormancy imposed on them for a longer time period than seed near the soil surface (Richardson and Kluge, 2008).

The seed of Australian *Acacia* can be divided into seed possessing eliasomes (ant dispersed) and seed possessing brightly coloured arils (bird dispersed) (Richardson and Kluge, 2008; Gibson *et al*., 2011). Seed with eliasomes are presented to ants for dispersal and consequent burial (Richardson and Kluge, 2008). The ant dispersed seed are also fire adapted (Richardson and Kluge, 2008) and require a heat pulse to break their dormancy (Jeffery *et al*., 1988). In the absence of fire, ant dispersed seed display high levels of viability and dormancy and low levels of germination and decay (Holmes and Moll, 1990). *Acacia baileyana, A. dealbata, A. decurrens, A. elata, A. implexa, A. longifolia, A. mearnsii, A. paradoxa, A. podalyriifolia* and *A. pycnantha* all have ant dispersed seed (Richardson and Kluge, 2008). Seed with brightly coloured arils are presented for dispersal by birds (Holmes and Moll, 1990). The ornithochorous seed germinate more readily after acid scarification (Pieterse, 1997), i.e. the digestive processes in animals, and also have lower heat requirement to break dormancy (Jeffery *et al*., 1988). Both types of seed are also passively dispersed for example by wind and water (Gibson *et al*., 2011). *A. cyclops* and *A. melanoxylon* have bird dispersed seed (Richardson and Kluge, 2008).

1.7. Port Jackson

1.7.1. Description

Acacia saligna, commonly known as Port Jackson, is a thornless willow-like leguminous shrub or tree normally reaching a height of between 3 - 7 m but may grow up to 10 m tall (Morris, 1991; Henderson, 2001). Leaves are replaced by phyllodes which are blue-green changing to bright green, having a length of up to 200 mm and a width of 10 - 50 mm, somewhat straight to drooping with one midvein, narrower and less wave-like on older plants (Henderson, 2001). In South Africa flowers are present during August to November in bright yellow circular inflorescences forming axillary racemes (Henderson, 2001). Seed are formed in initially green pods which turn brown, with hardened whitish margins as the legume matures (Doran *et al*., 1997; Henderson, 2001). In the pod dark brown to black glossy seed, 5 - 6 mm long and 3 - 3.5 mm wide, possessing a small funicle which inspissates into a cream coloured aril is carried lengthways (Doran *et al*., 1997).

Figure 1.2: Port Jackson willow, Ac. Saligna. (a) Flowering shoot; (b) mature phyllode; (c) mature pod (Morris, 1991); (d) pod capsule. (Drawn by R. Weber, National Botanical Institute, Pretoria.)

1.7.2. Origin

Port Jackson is a pioneer species (Milton, 1980; O'Sullivan *et al*., 2009) native to the winter rainfall region in the southwest of Western Australia (Maslin, 1974; Milton and Hall, 1981; Doran *et al*., 1997; O'Sullivan *et al*., 2009). *Acacia saligna* has substantial genetic diversity and grows rapidly in various environments, usually favouring locations which accumulate moisture in excess of rainfall (O'Sullivan *et al*., 2009). The tree is abundant on the nutrient deficient sandy soils of the Swan Coastal Plain from Gingin southwards to Busselton and on the denser clay soils as far north as the Murchinson River (Doran *et al*., 1997). The eastern boundary of its range is 200 km east of Esperance (Doran *et al*., 1997). *Acacia saligna*'s altitudinal range stretches from sea level to approximately 300 m (Doran *et al*., 1997). It has a preference for the warm, sub-humid and humid climatic zones, but also occurs in the higher rainfall areas of the semi-arid zone (Doran *et al*., 1997). This species is found in areas with a mean annual temperature of 13 – 21 ℃ with the minimum temperature of the coldest month being 2 – 10℃ and the maximum temperature of the warmest month being 26 – 36 ℃ (Marcar *et al*., 1995). Near the coast it's not exposed to frost but inland it may be subject to an average of 1 – 6 frost events (Doran *et al*., 1997). The tree is present in areas with a mean annual rainfall of 280 – 1210 mm (Marcar *et al*., 1995). *Acacia saligna* is adapted to a variety of soil types, particularly nutrient deficient and calcareous sands as well as fairly dense clays and on a range of podzolics (Doran *et al*., 1997). It's mainly present in the less dense areas of the dry sclerophyll forest or in temperate woodlands (Doran *et al*., 1997). In its distribution area where water is scarce it can also be found in semi-arid low woodlands and mallee communities, occasionally extending to heath communities (Doran *et al*., 1997). It is also frequently present in eucalypt woodland (Doran *et al*., 1997).

1.7.3. History, extent of invasion and weed status

According to Shaugnessy (1978) Port Jackson has been present in South Africa since 1833. *Acacia saligna* was used extensively during the 1840s and 1850s for sand dune stabilisation an activity that was practiced at least until 1978. *Acacia saligna* was among the material collected for the Cape Town Botanical Garden by 1858. The garden did not only acquire material of *A. saligna* but also facilitated its spread through distributing seed to the public. Port Jackson was also highly recommended by J.C. Brown a Botanist who widely promoted the cultivation of trees and shrubs in the Cape during the 1860s. After 1875 J.S. Lister established many pine plantations and Port Jackson was used in the plantations to shelter young pine trees. *Acacia saligna* was for a short period planted in the Cape Flats as a source of tannins for tanning leather. However, after a while black wattle was assessed to be superior for this use and large stands of Port Jackson were abandoned (Shaugnessy, 1978).

In the mid 1980s *A. saligna* was assessed to be potentially the most damaging invasive species in the coastal lowlands of the south-western Cape (Macdonald and Jarman, 1984; Van Wilgen and Richardson, 1985). After 25 years Port Jackson was rated as second of the 20 most prominent invaders in the fynbos biome (Henderson, 2007). In the west, south and eastern Cape coastal regions *A. saligna* has formed large dense stands (Fig. 1.2) over a vast area on conservation, water catchment and agricultural land (Richardson *et al*., 1992; Morris, 1997; Morris, 1999). This has resulted in the replacement of natural vegetation, alterations in ecosystem processes and interference with agricultural practices (Richardson *et al*., 1992; Morris, 1997; Morris, 1999).

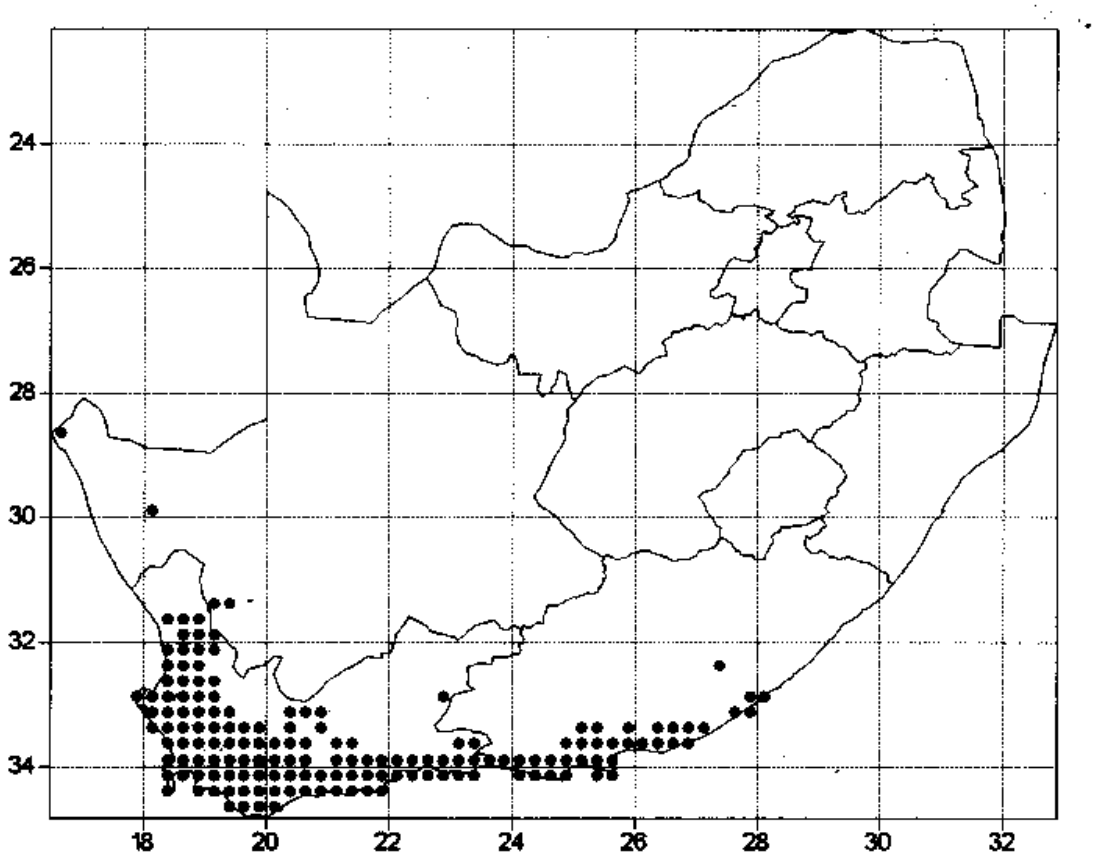

Figure 1.3: Distribution of *Acacia saligna* in South Africa. (Henderson, 2001).

(Drawn by L. Henderson, Plant protection research Institute, Pretoria.)

1.7.4. Phenology of *Acacia saligna*

1.7.4.1. Growth phenology of *Acacia saligna*

The growing season of *A. saligna* is influenced by water availability and temperature (Milton, 1980; Milton and Moll, 1982). Growth begins when the water in the soil available for use by plants is at a maximum and ends when available water is exhausted (Milton, 1980; Milton and Moll, 1982).

Where water is not a limiting factor and available throughout the year, the end of the growth season is determined by temperature (Milton, 1980; Milton and Moll, 1982). Under temperature limiting conditions, the growth season will end when temperatures are below 15 ℃ or less than 7.5 hours of sunshine per day (Milton, 1980; Milton and Moll, 1982). Consequently, in water limited conditions, water and temperature determines the length of the growing season (September-February, with spring growth peak) (Milton, 1980; Milton and Moll, 1982). However, in conditions where water is not limiting only temperature influence the growing seasons' length (August-April) (Milton, 1980; Milton and Moll, 1982). Therefore *A. saligna* occurring along river courses, near lakes and dams and in coastal regions is likely to have longer growing seasons and to grow faster than those growing in well drained soils (Milton, 1980; Milton and Moll, 1982). This implies that, in a summer drought climate, areas most vulnerable to invasion by *A. saligna* are those areas where growth is limited only by temperature (Milton, 1980; Milton and Moll, 1982).

Some Acacias show the capability to lengthen their growing season into summer when water is not limiting or to generate another growth effort in reaction to rain (Milton, 1980; Milton and Moll, 1982). In warm temperate climates Acacias can sustain some growth throughout the year (Milton, 1980; Milton and Moll, 1982), giving them the ability to react to unseasonal increments in rainfall or temperatures (Milton, 1980; Milton and Moll, 1982; Connor *et al.*, 1971). Acacias stop growing when temperatures drop to or below zero (Connor *et al.*, 1971).

Acacias are physiologically well adapted to warm dry climates (Milton, 1980; Milton and Moll, 1982). When the phyllodes experience negative turgor pressure due to late summer drought (Hellmuth, 1971), water-use efficiency increases, and the photosynthetic rate is not influenced (Milton, 1980). When temperatures do not fall within the 16 ℃ to 35 ℃ range, photosynthesis decreases to less than 50 % of the maximum (Van den Driessche *et al.*, 1971).

1.7.4.2. Litterfall phenology

The litter of *A. saligna* falls throughout the year (Milton, 1980; Milton and Moll, 1982). The total litter for Port Jackson has been recorded to be 8042 kg/ha/yr (Milton, 1980; Milton and Moll, 1982). Phyllodes form the largest component of the litter (60.8 %), followed by pods (12.1 %), wood (10 %), flowers (8.7 %) and seed (8 %) (Milton, 1980; Milton and Moll, 1982).

The addition of phyllodes to the litter occurs throughout the year with peaks during summer (November-March) (Milton, 1980; Milton and Moll, 1982). These peaks coincide with periods of water stress and growth (Milton, 1980; Milton and Moll, 1982). The loss of foliage when water is a limiting factor might be a response to decrease the rate of transpiration (Hanes, 1965). Losses as a consequence of active growth might be a result of internal nutrient cycling; an adaptation which is beneficial in nutrient poor soils (Milton, 1980; Milton and Moll, 1982).

Wood fall is very variable throughout the year and it has been suggested that large losses of woody material is a result of the first heavy winter rain, and to strong wind (Milton, 1980; Milton and Moll, 1982). Flower fall is strictly seasonal, with most of the flowers falling during spring. Three to four months after pollination the pods fall from the tree over a six week period. Pod and seed fall occurs simultaneously (Milton, 1980; Milton and Moll, 1982).

1.7.4.3. Reproductive phenology

Port Jackson trees forms flower buds during May, which is followed by a four month growth season (Milton, 1980; Milton and Moll, 1982). Anthesis takes place from August to September (Milton, 1980; Milton and Moll, 1982). The pods that are formed after the flowers have been pollinated grow over a period of four months (Milton, 1980; Milton and Moll, 1982). In December when the pods have reached maturity they dehisce and release their seed (Milton, 1980; Milton and Moll, 1982). The pods are then shed and by February all the pods have fallen from the trees (Milton, 1980; Milton and Moll, 1982). It was determined that only 10 % of the inflorescence per m^3 of *A. saligna* canopy bear pods (Milton, 1980; Milton and Hall, 1981). The seed in the canopy has been estimated to be 10 562 m^{-2} (Milton, 1980; Milton and Hall, 1981), while seed rain or fall has been recorded to be between 446 and 13 472 m^{-2} (Wood and Morris, 2007).

1.7.5. The seed bank

1.7.5.1. Dormancy

Most of the seed produced by *A. saligna* is enclosed with a water impermeable testa (Rolston, 1978; Milton and Hall, 1981; Holmes *et al*., 1987). Consequently the seed remain dormant, accumulating in the litter and soil to form a seed bank (Milton and Hall, 1981). The seed remain dormant in the seed bank until the testa is adequately damaged to allow water absorption (Milton and Hall, 1981), a process generally initiated by a heat pulse (Tran and Cavanagh, 1984; Jeffery *et al*., 1988). The lowest relative humidity experienced during ripening determines the dormancy of the seed (Tozer, 1996).

1.7.5.2. Seed bank size

Acacia saligna's soil stored seed banks vary in size and are determined by a large number of different factors including seed rain, the age of the stand, stand density or canopy cover, distance from canopy (Richardson and Kluge, 2008), duration of seed dormancy, predation, decay (Weaver

and Cavers, 1979; Milton and Hall, 1981), substrate type and degree of soil disturbance (Holmes and Cowling, 1997). The rate of seed accumulation increases with tree age until the trees reach an age of approximately 30 years where after seed accumulation rate stabilize (Milton and Hall, 1981). The seed banks of *A. saligna* in southern Africa have been recorded as being between 2 000 seeds m^{-2} (Morris, 1999; Strydom *et al*., 2012) and 212 000 seeds m^{-2} (Morris, 1997; Strydom *et al*., 2012).

1.7.5.3. Vertical and Horizontal Distribution

The largest proportion of *A. salignas* seed bank is situated below the litter but within the upper 10 cm of the soil (Milton and Hall, 1981; Strydom *et al*., 2012). The number of seed in the soil decrease with depth (Milton and Hall, 1981; Holmes, 2002; Strydom *et al*., 2012) and below the 10 cm mark the number of seed declines rapidly (Milton and Hall, 1981; Strydom *et al*., 2012). The nature of the soil will determine how deep seed penetrate into the substrate (Milton and Hall, 1981; Richardson and Kluge, 2008), with seed having been located at a depth of 35 cm in loose sandy soil (Milton and Hall, 1981; Strydom *et al*., 2012) and 80 cm in riparian soils (Esler and Boucher, 2004). In addition the movement of seed in the soil is influenced by dispersal vectors (e.g. ants and water), soil organisms (e.g. mole rats), substrate type (Milton and Hall, 1981), percolation of water and openings left in the soil for example by decomposing roots (Harper, 1977). It has been concluded that the horizontal distribution of the seed bank of alien *Acacia* in southern Africa is even (Milton and Hall, 1981), however a more recent study has found the seed in the upper soil layer to be clumped (Strydom *et al*., 2012). *Acacia* species tend to have a clumped distribution in Australian soils which is attributed to storage of seed by ants in their nests (Majer, 1978).

1.7.5.4. Dispersal

The number of seed declines sharply past the edge of the vertical projected canopy of alien *Acacia* trees (Milton and Hall, 1981). This is the result of *Acacia* seed dropping straight to the ground (Milton and Hall, 1981). Where areas with slopes are concerned, the seed tend to accumulate at the base of the slope (Milton and Hall, 1981). The seed of *A. saligna* is also dispersed along streams and rivers (Milton and Hall, 1981).

1.7.5.5. Viability

Most of the *A. saligna* seeds are viable (86 – 100 %) (Milton and Hall, 1981; Holmes *et al*., 1987). Seed in the litter and soil have the same order of dormancy and viability as mature seed in the canopy (Milton and Hall, 1981). After germination requirements have been met, seed deeper in the

soil profile germinate faster than seed near the soil surface (Milton and Hall, 1981). However, seedlings of seed situated near the surface are more vigorous than seedlings of seed situated deeper in the soil profile (Milton and Hall, 1981).

1.8. Management options for *Acacia saligna*

Seed production, seed dispersal, seed banks, seedling establishment and sapling or adult growth, constitute the different stages during which measures can be applied to control *A. saligna* populations (Wilson *et al*., 2011). Seed produced by *A. saligna* populations are reduced by two biological control agents, *U. tepperianum* and *M. compactus* (Wood and Morris, 2007). Once seed are released from trees the biological control agents of *A. saligna* have no further effect. There are no measures currently available to decrease seed being released during the seed dispersal phase (Richardson and Kluge, 2008). Fire is used to reduce seed residing within the litter layer (Richardson and Kluge, 2008). The seed in the upper seed bank (top 15 cm) may be reduced by fire or solarisation (Richardson and Kluge, 2008). Seedlings as well as saplings and older trees may be killed through mechanical (hand pulling etc.) or chemical measures (herbicides) (Morris, 1991). Depending on capacity (manpower, equipment, money etc.) and practicality (extent of *A. saligna* population in an area), mechanical and chemical measures can be applied during every phase (Morris, 1991).

1.8.1. Biological control

Two biological control agents (*Uromycladium tepperianum* and *Melanterius compactus*) have been released as natural enemies for *A. saligna* populations in South Africa (Morris, 1991; Morris, 1999; Wood and Morris, 2007). Indigenous to Australia, *U. tepperianum* is a gall inducing rust fungus that attacks young expanding phyllodes, stems and reproductive tissue (Morris, 1991). The gall rust fungus places its host under stress leading to reduced phyllode, flower and pod production and making infected *A. saligna* individuals more vulnerable to stress factors e.g. drought (Morris, 1991; 1999). *Uromycladium tepperianum* has decreased stand density (to 5 – 10 % of original stand density) (Morris, 1999), canopy density and seed production (Wood and Morris, 2007).

Melanterius compactus is a seed feeding weevil and was introduced into South Africa to compliment the impact of the gall inducing rust fungus through further reduction of seed production levels (Wood and Morris, 2007). Mature *M. compactus* individuals oviposit in and feed on developing *A. saligna* seed pods (Impson *et al*., 2011). A small hole in the wall of a swollen green pod capsule (pods consist of several capsules) is made, through which one egg is generally inserted (Impson *et al*., 2004). The egg is positioned on or close to the developing seed within the

pod capsule (Impson *et al*., 2004). After hatching the larva will burrow into the developing seed (Impson *et al*., 2004). The entire seed content is consumed during this time, with only the hard seed coat remaining (Impson *et al*., 2004). The fully developed larva exits the pod capsule and falls to the ground where it pupates in the soil (Impson *et al*., 2004). Most adult weevils emerge within 6 - 8 weeks and overwinter under the loose bark of trees or stay within the soil for this period (Impson *et al*., 2004; Impson *et al*., 2011). *Melanterius compactus* may live for two years (Denhill *et al*., 1999) and usually have slow dispersal rates (approximately 2 km per year) (Impson *et al*., 2004). *Melanterius compactus* is the most successful weevil of all the *Melanterius* species released in South Africa as biological control agents (Impson *et al*., 2011). Where it has established *M. compactus* is observed as considerably reducing seed rain and is described as having damage levels of 90 % regularly (Impson *et al*., 2011). In South Africa it has been released in 18 sites, 3 in 2001, 2 in 2003 and 13 since 2004 (Impson *et al*., 2011).

1.8.2. Fire

Management with fire is the most successful method to reduce *A. saligna* seed bank densities (Holmes, 1988; Richardson and Kluge, 2008). Fire decreases seed bank size through destroying seed or stimulating germination (Milton and Hall, 1981; Holmes, 1988; Cilliers *et al*., 2004). Slow, hot fires are more effective than rapid fires to achieve these results (Milton and Hall, 1981; Cilliers *et al*., 2004). Fire management will be more efficient in reducing seed density in areas were the seed bank is primarily situated near the soil surface (Esler and Boucher, 2004).

Care should be taken when managing Port Jackson populations with fire (Van Wilgen *et al*., 1994; Cilliers *et al*., 2004) as they have higher fuel loads than the native communities which may lead to unnaturally intense fires (Cilliers *et al*., 2004). The consequence of such fires can be destruction of regenerative subterranean organs, native seed banks loss (Musil and Midgley, 1990; Holmes, 2002; Cilliers *et al*., 2004) soil structure damage, soil sterilization (Van Wilgen *et al*., 1994; Campbell *et al*., 1999) and ultimately reduced diversity and native population recovery (Van Wilgen *et al*., 1994; Holmes, 2002; Cilliers *et al.,* 2004; Richardson and Kluge, 2008). In addition, to the fuel load *of A. saligna* populations, fire intensity will be influenced by fire duration, season of fire event, site topography and climatic conditions on the day of burning (Van Wilgen, 1984; Van Wilgen *et al*., 1992; Cilliers *et al*., 2004). Furthermore *A. saligna* seed may survive higher fire intensities than seed of native species (Jeffery *et al*., 1988).

Managers should therefore determine the season including the period within a season when a fire is most likely to have the desired intensity, maximising fire efficiency and minimizing associated risks (Van Wilgen *et al*., 1992; Van Wilgen *et al*., 1994). Furthermore season will also influence whether indigenous species as well as *A. saligna* seed germinating after fire will be able to

establish successfully (Milton and Hall, 1981). In addition to selecting favourable conditions, clearing techniques preceding burning can be manipulated, to ensure burning will result in the desired outcomes. Burning methods include “fell and burn”, “stack and burn”, “fell, remove and burn” and “burn standing” (Milton and Hall, 1981; Holmes *et al*., 1987; Cilliers *et al*., 2004). The merit of these methods will depend on the extent, population age and the location (easy accessible or not) of *A. saligna* infestations as well as the desired management outcomes. After these methods have been applied follow up treatments are crucial (Milton and Hall, 1981; Holmes *et al*., 1987; MacDonald and Wissel, 1992), as germinating seedlings will lead to the development of new *A. saligna* populations (Holmes *et al*., 1987). Hand pulling, herbicide application or selective grazing can be used to remove seedlings depending on the extent of the regenerating *A. saligna* population (Campbell *et al*., 1999; Richardson and Kluge, 2008). Restoration programmes are crucial for the faster and successful rehabilitation of areas after alien vegetation has been removed (Holmes and Cowling, 1997b; Holmes, 2002; Vosse *et al*., 2008).

1.8.3. Solarisation

This technique entails heating the upper part of the soil to between 40 and 70 ˚C through covering the soil surface with plastic sheeting (Cohen *et al*., 2008; Richardson and Kluge, 2008). Soil temperatures acquired by this method may lead to decreased seed viability or stimulate seed germination (Edgely, 1983). In Israel it has been proven to be effective in reducing the seed banks of *A. saligna* up to 12 cm below the soil surface (Cohen *et al*., 2008). The method is however limited in the extent that it can be applied (Richardson and Kluge, 2008). Solarisation may be useful in reducing seed banks in sensitive habitats (Richardson and Kluge, 2008), although secondary impacts would need to be carefully managed.

1.8.4. Mechanical and chemical control

Mechanical methods assessed to be most effective in controlling *A. saligna* populations are: hand pulling seedlings, digging out entire plants and debarking to soil level (Morris, 1991). Implementing fire to control seedlings or mature plants is only moderately efficient (Morris, 1991). The application of herbicides to cut stumps and spray to coppicing individuals or seedlings was assessed to be moderately effective (Morris, 1991). Mechanical and chemical control is associated with high costs and consequently is only feasible in valuable conservation and intensively farmed areas (Morris, 1991). Where *A. saligna* occurs there are few areas where these populations are actively being managed (Morris, 1991).

1.9. References

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Chapter 2: Seed production of *Acacia saligna*: an assessment of size and variation over a geographical range in South Africa

Abstract

Port Jackson is a small leguminous shrub or tree native to south-western Australia and is potentially the most damaging invasive plant in the coastal lowlands of the south-western Cape, South Africa. Despite extensive mechanical and biological control, high levels of reproduction and resultant seed banks remain a challenge for management. To gain a spatial understanding of the conditions under which the species is likely to produce the most seed, this study quantified reproductive output over its invaded distribution range and determined the influence of various environmental and biological factors on reproduction. Seed pod rain and seed rain was measured in dense, monospecific stands across a range of abiotic and biotic conditions. Despite control measures Port Jackson trees still produce large quantities of seed. The size of the reproductive output is largely influenced by water availability, with Port Jackson populations in more arid environments producing less seed than in environments where water is more readily available.

Key Words: Invasive alien plant, Reproductive output, Environmental conditions

2.1. Introduction

Acacia saligna (Port Jackson) is one of several invasive Australian *Acacia* species that pose serious threats to the unique biodiversity of the Cape Floristic Region (Richardson and Kluge, 2008; Gibson *et al*., 2011). Despite management efforts over the past two decades, Port Jackson remains a prominent feature of the vegetation in the Western and Eastern Cape of South Africa. The success of this Australian weed can be ascribed to its large persistent seed banks (Richardson and Kluge, 2008). The seed banks of *A. saligna* are the consequence of its seed rain and the ability of the seeds to remain dormant for long time periods. Seed rain can be defined as the initial dispersal of propagules from their point of origin towards the earth. Initial dispersal may be the consequence of abiotic (e.g. wind) or biotic (e.g. birds) factors (Harper, 1977). The seed rain of *A. saligna* has received little attention and only a handful of studies have attempted to estimate seed production (Milton and Hall, 1981; Holmes, 1990; Wood and Morris, 2007). Gibson *et al*., (2011) also acknowledge this lack of data for reproductive traits of invasive and non invasive *Acacia* species. Biotic factors affecting the seed rain of *A. saligna* have received some attention but the influence of abiotic conditions has largely been neglected. Therefore processes affecting the reproduction of *A. saligna* are poorly understood. Furthermore seed rain estimations of

previous studies do not cover the entire distribution range of this invader. Spatially explicit information is required to form a general understanding of how the seed rain of *A. saligna* varies across different environmental gradients and with stand age. This study will help further our understanding of factors increasing invasiveness which has been highlighted as essential for reducing invasive success and achieving management objectives (Wilson *et al*., 2011).

Alien plants must be able to establish and survive in an introduced environment in order to be able to reproduce. Establishment in novel environments requires alien species to cope with or adapt to prevailing environmental conditions (Wiether and Keddy, 1995; Catford *et al*., 2009). In general, plant growth may be limited by climatic (Milton and Hall, 1981; Gutiérrez *et al*., 2000; Goal and Fox, 2002; Zegada-Lizarazu *et al*., 2007; Caballero *et al*., 2008), topographic (Caballero *et al*., 2008), edaphic (Witkowski, 1991; Yelenik *et al*., 2004; Fravolini *et al*., 2005; Medinski *et al*., 2010) and biotic conditions (Morris and Wood, 2007). Climatic limitations are normally the most important as plants directly or indirectly depend on the atmosphere for successful growth and reproduction (Schulze and McGee, 1978). Furthermore, plants differ in their requirements for, and tolerances of, specific climatic conditions (Schulze and McGee, 1978; Tainton and Hardy, 1999; Medinski *et al*., 2010). Consequently, climatic conditions are important for determining where plants can exist (Schulze and McGee, 1978). Rainfall is regarded as the climatic parameter which most clearly determines plant community distribution in South Africa (Schulze and McGee, 1978; Tainton and Hardy, 1999). Water is often a restricting factor during plant development and is crucial for maintaining physiological and chemical processes within plants, including germination, growth and reproduction (Schulze and McGee, 1978). Soil is the medium through which plants have access to water received through rainfall and consequently edaphic factors will influence the water available for their use.

Soil water availability possibly exerts the largest pressure on plant growth in arid and semi-arid regions (Cody, 1989). Soil-water relationships, aeration and penetrability of soils are directly influenced by soil texture (Etherington, 1975). The effect texture has on these factors is a consequence of the relationship between texture and interparticle pore space (Etherington, 1975). The infiltration rate of water is usually lower in finer textured soils during rainfall (Fravolini *et al*., 2005), increasing run-off (Etherington, 1975). Finer textured soils are also more prone to crust formation (Medinski *et al*., 2010), reducing water percolation into the soil and further increasing run-off (Rao *et al*., 1998). Soil texture also influences the location where water is stored (Medinski *et al*., 2010). Coarse textured soil stores water deeper in the soil profile than finer textured soils which favours woody vegetation with deeper roots (Sala *et al*., 1997). Furthermore fine textured soils lose more water to evapotranspiration than coarse textured soils as a consequence of their shallower water storage (Fravolini *et al*., 2005). The climatic and edaphic conditions of an area will consequently be crucial in determining the resources (e.g. water) that are available for plants.

Generally, plants allocate resources which they accumulate to growth, maintenance and reproduction (Harper, 1977; Stephenson, 1981). Resources are required to produce fruit and seed (Stephenson, 1981). Fruits are dependent on leaves for carbohydrates and nutrients (Hocking and Pate, 1977). Generally fruit acquire resources from the closest leaves, but they may receive resources from leaves a meter or so away (Mooney, 1972). Therefore, each reproductive structure and its neighbouring leaves may be regarded as an independent unit in terms of assimilates supplied by the leaves (Harper and White, 1974). The reproductive structures may also use resources accumulated in previous years and stored in perennial tissues (Kozlowski and Keller, 1966). All reproductive structures drawing upon resources together with the total resources of the individual or branch determine the resources available to a given flower or fruit (Stephenson, 1981). Plants balance reproductive output with available resources through flower and juvenile fruit abscission (Stephenson, 1981). Various species generally form mature fruits from only a small percentage of their flowers (Stephenson, 1979). These species frequently abscise flowers and immature fruits and *Acacia* appear to be part of this category (Goal and Fox, 2002). Therefore the climatic and edaphic conditions of an area will indirectly influence the reproduction of plants through influencing the amount of resources that are available for their use. Consequently abiotic factors, to which a plant is adapted, are important in assessing where plants may occur as well as the size of their reproductive output.

In south-western Australia *A. saligna* has a preference for warm, sub-humid and humid climatic zones, but also occurs marginally in the semi-arid zone (Doran *et al*., 1997). This species is found in areas with a mean annual temperature of 13 – 21 °C with the minimum temperature of the coldest month being 2 – 10 °C and the maximum temperature of the warmest month being 26 – 36 °C (Marcar *et al*., 1995). Near the coast it is not exposed to frost but inland it may be subject to an average of 1 – 6 frost events p.a. (Doran *et al*., 1997). The tree is present in areas with a mean annual rainfall of 280 – 1 210 mm (Marcar *et al*., 1995) and these areas receive most of their precipitation during winter (Doran *et al*., 1997; O'Sullivan *et al*., 2009). *Acacia saligna* is adapted to a variety of soil types, particularly nutrient deficient and calcareous sands as well as fairly dense clays and on a range of podzolics (Doran *et al*., 1997). In its invaded habitat in South Africa, Port Jackson is restricted primarily to the coastal plain regions with an annual rainfall of more than 250 mm (Cronk and Fuller, 1995). The climate of the areas in South Africa where *A. saligna* occurs is similar to its native range (Cronk and Fuller, 1995). In addition to the abiotic conditions to which *A. saligna* is adapted to, its biology and other biotic factors influencing its growth and reproduction will also be crucial in understanding its reproductive output.

In its native environment *A. saligna* populations reach an age of approximately 20 years under favourable conditions with a 5 to 12 year life-span considered to be the norm (O'Sullivan *et al*., 2009). Tree longevity, in its native range, was observed to decline with decreasing latitude and the decrease in longevity was ascribed to higher temperatures and evaporative demand (O'Sullivan *et*

al., 2009). Other key limiting factors to tree longevity include insect attack and infection *by Uromycladium tepperianum* (O'Sullivan *et al*., 2009). In South Africa trees were estimated to reach an age of between 30 – 40 years in the absence of natural enemies (Milton and Hall, 1981). However, two biological control agents (*U. tepperianum* and *Melanterius compactus*) have been released in South Africa since then as natural enemies (Morris, 1991; Morris, 1999; Wood and Morris, 2007; Impson *et al*., 2011). After 30 years in the presence of the gall rust fungus *A. saligna* trees are estimated to rarely reach an age older than 10 years (Wood and Morris, 2007).

Indigenous to Australia, *U. tepperianum* is a gall inducing rust fungus that attacks young expanding phyllodes, stems and reproductive tissue (Morris, 1987; Morris, 1991). *Uromycladium tepperianum* on Port Jackson may be annual or perennial (Morris, 1991) and gall rust spores are wind dispersed (Morris, 1999). The gall rust fungus place its host under stress leading to reduced phyllode, flower and pod production which makes infected *A. saligna* individuals more vulnerable to stress factors e.g. drought (Morris, 1991; Morris, 1999). Severely affected plants often bear few phyllodes and form few flowers and pods (Morris, 1987). Since its release in 1987 (Morris, 1991) *U. tepperianum* has decreased seed production (Wood and Morris, 2007), stand density (Morris, 1997; 1999) and canopy density of *A. saligna* populations (Wood and Morris, 2007). Higgins *et al*., (1997) estimated that it would take twenty five years for large and mature *A. saligna* populations to decline to low population levels in the presence of *U. tepperianum* and fire. The gall rust fungus is present wherever the tree occurs in South Africa (Wood and Morris, 2007).

Melanterius compactus, a seed feeding weevil, was introduced into South Africa to compliment the impact of *U. tepperianum* through further reducing seed production levels (Wood and Morris, 2007). Mature *M. compactus* individuals oviposit in and feed on developing *A. saligna* seed pods (Impson *et al*., 2011). *Melanterius compactus* may live for two years (Denhill *et al*., 1999) and usually have slow dispersal rates (approximately 2 km per year) (Impson *et al*., 2004). *Melanterius compactus* is the most successful weevil of all the *Melanterius* species released in South Africa as biological control agents (Impson *et al*., 2011). Where it has established *M. compactus* is observed as considerably reducing seed rain and is described as having damage levels of 90 % regularly (Impson *et al*., 2011). In South Africa it has been released in 18 sites, 3 in 2001, 2 in 2003 and 13 since 2004 (Impson *et al*., 2011).

Acacia saligna plants are able to produce seed in the second year after germination but only produce large seed crops after 5 years (Milton and Hall, 1981). The ability to produce large quantities of seed within a relatively short time period has been assessed as being crucial for invasion success of Australian *Acacia* (Gibson *et al*., 2011). Wet winter conditions are needed to induce flowering and precipitation is essential after flowering to encourage pod development and good seed set (Gaol and Fox, 2002). Trees flower with the onset of spring (August to September) (Milton, 1980) and less than 1 % of the flowers produce mature pods (Milton and Hall, 1981). Pods

reach maturity at the start of summer (December) after which they dehisce and release their seed and all pods are shed by late summer (February/March) (Milton, 1980). Seed rain of *A. saligna* varies in size and is determined by stand age, stand density, predation (Milton and Hall, 1981; Richardson and Kluge, 2008), phyllode number and number of new shoots formed within a season (Gaol and Fox, 2002). Before *U. tepperianum* was released in South Africa the seed in the canopy was estimated to be 10 562 m^{-2} and the seed rain to be 5 443 m^{-2} for mature trees and 530 m^{-2} for saplings (Milton and Hall, 1981). The seed rain has since been recorded to between 2 645 m^{-2} and 13 472 m^{-2} for four sites in 1989 (Wood and Morris, 2007), 2 102 m^{-2} for one site in 1990 (Homes, 1990) and between 446 m^{-2} and 3 035 m^{-2} for four sites in 2004 (Wood and Morris, 2007); there is therefore some indication that biological control has reduced seed output to a certain extent. However, it should be noted that these estimations were made under stands of different ages and environmental conditions.

The aim of this study was to estimate the seed production of *A. saligna* across its invaded range in South Africa in order to gain a spatial understanding of the conditions under which the species is likely to produce the most seed. In order to achieve this, pod and seed rain was measured in dense, monospecific stands across a range of abiotic and biotic conditions. The study aimed to answer the following questions:

1) What is the status of the seed rain of *A. saligna* across its distributional range?

2) What is the effect of different environmental factors on seed production?

Before the study was undertaken, predictions were made that seed production will be the largest in older *A. saligna* populations with low gall rust infection and weevil predation, longer invasion histories and time since last fire, receiving more rainfall throughout the year and situated on more coarse textured soil.

2.2. Methods

2.2.1. Study Site selection

Throughout the current total distribution of *A. saligna,* potential sites were identified on the basis of being monospecific and relatively dense (i.e. closed canopy). Monospecific stands were selected to prevent the influence of interspecific competition on the data, to reduce factors playing a role on the pod capsule and seed rain and to create more controlled circumstances. After potential sites had been identified the actual sites were selected to include as much environmental variation as

possible. According to the above mentioned criteria ten sites were selected for the seed rain experiment (Figure 2.1 and Figure 2.2).

2.2.2. Site location

All of the sites except Welgelegen, the Eastern Cape site, are situated in the Western Cape. The Western Cape sites can be grouped into sites located along the west and south coast. The sites along the west coast, except Travellers Rest, lie 12 – 45 km from the coast and between the coast and the north-south ranges of the Cape Fold Mountains. Travellers Rest is situated in the Agterpakhuis region on the eastern side of the Cederberg. In contrast, the sites along the south coast lie 2 – 39 km from the coast and between the coast and the west-east ranges of the Cape Fold Mountains. The site in the Eastern Cape is situated near Oesterbay 2 km from the coast and between the coast and the eastern edge of the Outeniqua Mountains. Sites can also be divided into coastal and inland sites. Four of the ten sites, Travellers Rest, Locheim, Bossiesvlei and Fairfield, can be classified as inland sites (more than 25 km from the coast). Furthermore there are three sites, Travellers Rest, Rietvlei and Fairfield, situated along watercourses and one site, Bossiesvlei, situated along a gully.

2.2.3. Seed and pod rain sampling

The pod capsule rain and seed rain status of study sites was assessed through the use of seed rain traps. A trap consisted of a gauze bag fastened to the bottle neck opening of a plastic 2l soft drink bottle, which had been cut in half. Each trap was fitted into a PVC pipe (32 cm in length and 10.5 cm in diameter) with the bottle opening facing downwards in the pipe. The unit was secured to the PVC pipe with the end of the gauze bag 5 cm from the end of the pipe. Traps were secured at the soil surface, by fastening each with cable ties to two metal stakes which were driven into the ground with a hammer (Figure 2.2). At each site five *A. saligna* trees along a 20 m transect were selected at 5 m intervals around which traps were placed. Traps were placed approximately 1.5 m from the base of selected *A. saligna* trees (under their canopy) in a circle (Figure 2.2), giving a total of 25 traps per site. Traps were placed out during November 2010 (pre-dehiscence) and collected the following year during April 2011 (post-dehiscence) (Milton, 1980; Holmes, 1990a; Holmes, 1990b). The number of seeds and pod capsules in traps were recorded.

Figure 2.1: Satellite map displaying the location of the ten study sites. TR – Travellers Rest; RV – Rietvlei; BV – Bossiesvlei; LH – Locheim; SW – Swartwater; BP – Burgerspos; BR – Buffelsrivier; HV – Haasvlakte; FF – Fairfield; WL – Welgelegen. Yellow – West coast coastal sites, Green – West coast inland sites, Dark blue – South coast coastal, Light blue – South coast inland, Red – Eastern Cape sites, White – Sites on eastern side of the Cape Fold Mountains.

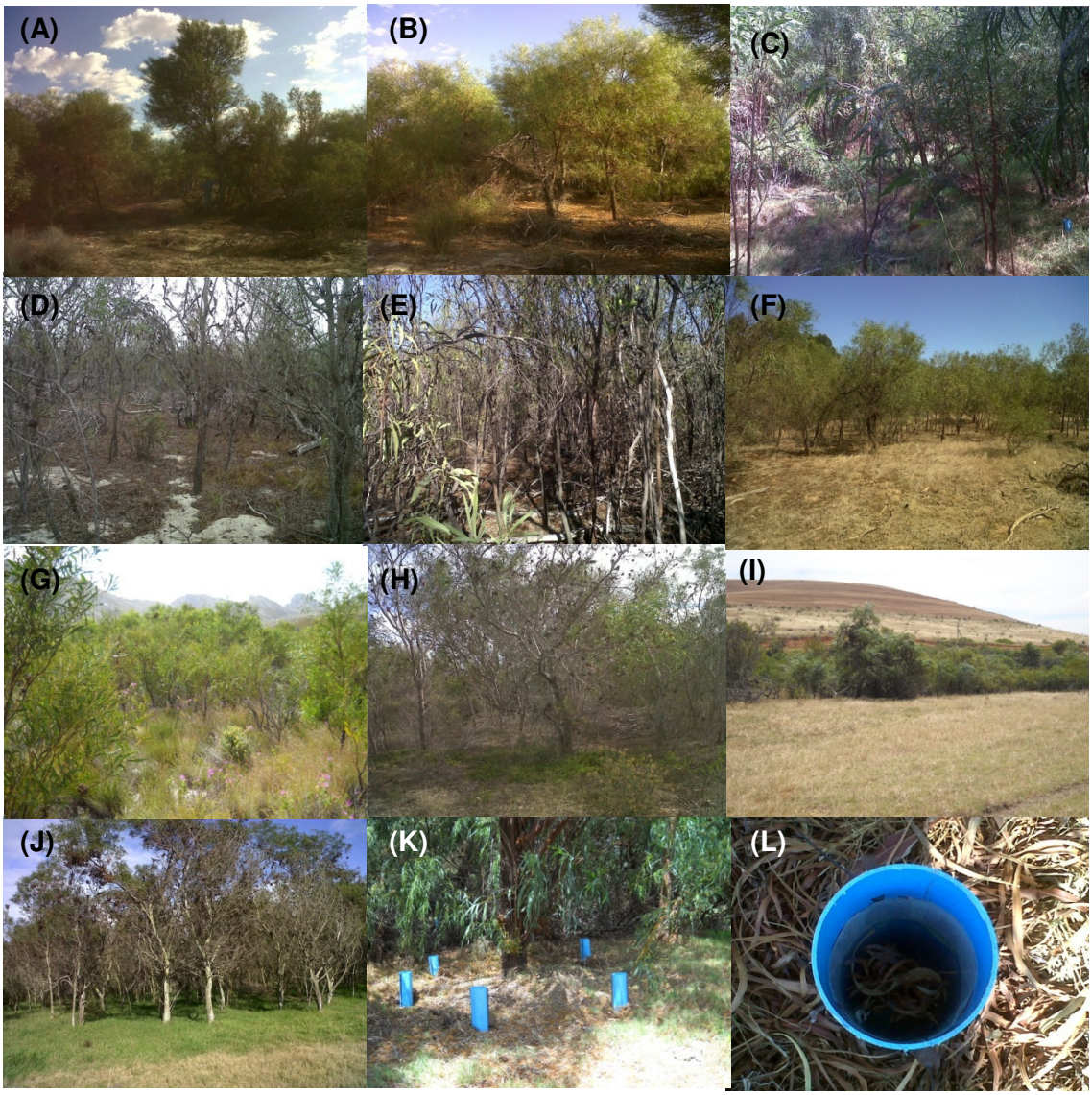

Figure 2.2: Photos illustrating the *A. saligna* populations of Travellers Rest (A and B), Rietvlei (C and K), Swartwater (D), Burgerspos (E), Locheim (F), Buffelsrivier (G), Haasvlakte (H), Fairfield (I) and Welgelegen (J). Photo (A) illustrates that *A. saligna* can still reach heights of 6 m or more under favourable conditions (man beside tree 1.91 m). Photo G is illustrative of *A. saligna* replacing the unique and aesthetic pleasing vegetation of the Cape Floristic Region. Photo (K) illustrates how traps were placed around the trees and photo (L) illustrates how the traps were assembled.

The average number of pod capsules and seed m^{-2} were calculated for every site as an estimate of seed production. Number of pod capsules was first divided by two before being averaged to get an approximation of the seed production. The pod capsule rain and seed rain were also tested for correlation with the Pearsons statistical test to assess whether the size estimated for seed production by these methods are comparable and therefore whether these methods estimate seed production with the same accuracy. The correlation between pod rain and seed rain was also used to determine whether the seed and seed pods fall in a similar pattern. Furthermore the pod capsule

and seed rain data were subjected to an Anova test to determine whether sites are different in terms of these measurements. If sites were different in terms of pod capsule rain or seed rain, these data were subjected to a multiple comparison of treatment by means test.

2.2.4. Biotic Factors

2.2.4.1. Tree size and density

At each site the circumferences of one hundred randomly selected *A. saligna* trees were measured at breast height to determine tree size. The number of steps taken and the direction of movement between trees were determined from a random numbers table. The tree circumference was then expressed as tree diameter. In addition to being a measurement of size these data serve as a proxy of tree age (Wood and Morris, 2007). At every site the density of the Port Jackson trees were also estimated through counting the number of trees within five randomly placed 5 x 5 m plots; density data were expressed as the number of trees per hectare. Furthermore tree circumference and tree density data were subjected to an Anova test to determine whether sites are different in terms of these measurements. If sites were different in terms of tree circumference or tree density, these data were subjected to a multiple comparison of treatment by means test. The tree diameter and tree density of the sites were also tested for correlation with Pearsons test. Rietvlei was omitted in this test as the site is an outlier in terms of its tree density, with a recent fire not having killed all the trees. The fire was also not hot enough to stimulate germination throughout the site. Where possible at each site, landowners provided information about invasion history, stand age and time since last fire. Supplementary information was obtained through satellite photos and previous published data was used to determine site history in these respects.

2.4.2.2. *Melanterius compactus*

The presence of *M. compactus*, the seed feeding weevil, was established by the presence of emergence holes in the pod capsules. The number of emergence holes in the pod capsules were counted, and expressed as a percentage of the number of pods to serve as an estimate of the damage done by the seed weeding weevil on seed production. This measurement estimates a minimum percentage damage level by the weevils, as the larvae may damage more than one seed in some cases or vacate the seed after the pod has dehisced. However, an idea of the accuracy of the predicted weevil damage levels can be gained by comparing the seed rain with the pod capsule rain minus the estimated weevil damage levels. Furthermore, the higher the predicted weevil damage levels are, the greater the difference between the seed rain and pod rain minus the

estimated weevil damage levels should be. The greater difference between the two estimates will be the consequence of the decrease in the probability of the seeds falling into the traps.

2.4.2.3. *Uromycladium tepperianum*

To determine gall rust severity, at every site the number of galls on a hundred trees were estimated. Trees were selected by the random sampling technique as described above. Trees were visually rated and assigned to one of the following classes of galls per tree: 0 - 20, 21 - 50, 51 - 100, 101 - 200, 201 - 500, 501 - 1000, 1001 - 2000, 2001+ (Morris, 1997). The total number of trees in each class was multiplied with the median value of the class, for example if there were five trees with galls falling in the 0 - 20 class then the calculation would be 5 × 10 = 50. The totals for all classes were summed and divided by one hundred to get an estimate of the average number of galls per tree at the site.

2.2.5. Abiotic Factors

2.2.5.1. Climatic Parameters

Weather data were acquired from Weather SA and the ARC-ISCW. Weather data for selected sites were chosen if the weather station was within 25 km from study sites and situated at approximately the same altitude. The long-term averages of the climatic parameters were used. Although current climatic conditions have a large influence on the reproductive effort of a plant, past climatic conditions will have influenced growth rates and resource storage during previous years and thus will have influenced the current reproductive potential of the plant (especially the number of shoots available for reproduction). The average should also be represtative of the climatic conditions of the years during which the study was conducted. Furthermore the environmental gradient rather than specific values are more important as different *A. saligna* populations in South Africa were compared over the invader's distribution range in the country. De Martonnes aridity index, summer aridity index, the winter concentration of precipitation and the minimum temperature of the coldest month was calculated for selected sites from the weather data. These parameters were used to indicate which localities present optimal conditions for *A. saligna* reproduction (Rutherford and Westfall, 1986). The altitude for every study site was determined through the use of a GPS.

2.2.5.2. Soil texture

Fifty soil samples were taken and bulked at each study site to assess soil texture. Sampling locations were determined through the random sampling technique as described above. The soil samples were given to the Soil Science Department at the University of Stellenbosch for analysis. They evaluated the soil texture according to the standard physical separation technique.

2.2.6. Climatic Indices

2.2.6.1. Winter concentration of precipitation (WCP)

The winter concentration of precipitation is a measure of the seasonality of rainfall (Bailey 1979). Winter concentration of precipitation is described by:

$$R = \frac{100\ (\text{sum of winter half precipitation})}{(\text{mean annual precipitation})}$$

with the sum of winter half precipitation being equal to the sum of the rainfall during April-September in mm.

2.2.6.2. De Martonne Aridity Index (DMAI):

De Martonne (1925) proposed the following equation to describe the aridity of a region:

$$H = \frac{P}{T+10}$$

where P is the annual precipitation in mm and T is the annual mean temperature in degrees centigrade. This index measures the precipitation effectiveness or aridity in a locality. Aridity is the extent to which a climate is deficient in life-promoting moisture (American Meteorological Society, 2011).

2.2.6.3. Summer aridity index (SAI)

The SAI is defined as “the sum of the mean precipitation for the four hottest months of the year, taken as a natural logarithm for scaling purposes and subtracted from a constant to ensure ascending values with increasing aridity” (Westfall and Rutherford, 1986).

The index is summarized by:

$$SAI = 9 - \ln\left[\sum_{i=1}^{4} Pi\right]_{t_{max}}$$

where P is mean monthly precipitation in mm and the four hottest months in the study area are December–March. The index is an indication of the moisture content of the atmosphere during a period of the year that is physiological important including under conditions of high evaporation demand (Westfall and Rutherford, 1986).

2.2.7. Data analysis

Data were analyzed with the statistical software package R (R core development team, 2011). Generalized mixed model analyses were also done to compare the seed pod rain and seed rain with the various abiotic and biotic variables. However, the degrees of freedom were too low for the full model to be used and the data set was also too small to compensate for the influence of the watercourses and the Eastern Cape site (Welgelegen) on the calculations (Appendix A). However, as previously discussed in section 2.2.3., through the use of an Anova test and multiple comparison of treatment by means, test sites could be compared and inferences made.

2.3. Results

The abiotic and biotic factors are described first to illustrate the climatic and edaphic patterns that exist over the distribution of *A. saligna* in South Africa, as well as the biological characteristics of the current *A. saligna* populations at the study sites. Next, the seed pod capsule and seed rain status of the *A. saligna* populations are reported to show how seed production follows or fluctuates with these climatic, edaphic and biological conditions. Furthermore, the seed pod capsule and seed rain estimates of sites for every category (e.g. west coast inland, west coast coastal, south

coast inland etc.) was compared through the use of tables to make the patterns apparent as there were too few sites per category to draw meaningful graphs.

2.3.1. Environmental Factors

In general inland sites are located at higher altitudes (average altitude of inland sites = 181 m) than coastal sites (average altitude of coastal sites = 85 m) (Table 2.1). When sites with similar distances from the coast are compared, sites along the west coast tend to be situated at higher altitudes than sites along the south coast. No clear pattern is apparent for the temperature of the coldest month (TCM).

Table 2.1:
Altitude (Alt), De Martonnes aridity index (DMAI), summer aridity index (SAI), mean annual precipitation (MAP), winter concentration of precipitation (WCP), mean annual temperature (MAT) and the temperature of the coldest month (TCM) for ten *A. saligna* populations in South Africa.

Site	Co-ordinates	Alt (m)	DMAI	SAI	MAP (mm)	WCP (%)	MAT (˚C)	TCM (˚C)	River or Stream
Travellers Rest	S 32° 04' E 19° 04'	314	7.9	5.58	235	78	20	7	River
Rietvlei	S 32° 38' E 18° 30'	130	11.5	5.30	323	74	18	6	Stream
Bossiesvlei	S 33° 12' E 18° 40'	158	14.7	5.18	422	79	19	8	No
Locheim	S 33° 13' E 18° 40	132	14.7	5.18	422	79	19	8	No
Swartwater	S 33° 16' E 18° 15'	91	16.3	5.31	456	79	18	8	No
Burgerspos	S 33° 31' E 18° 32'	114	23.9	5.19	668	83	18	8	No
Buffelsrivier	S 34° 20' E 18° 51'	66	19.6	4.90	545	72	18	9	No
Fairfield	S 34° 24' E 19° 48'	120	14.8	4.51	398	61	17	5	Stream
Haasvlakte	S 34° 36' E 19° 52'	42	20.1	4.54	546	66	17	9	No
Welgelegen	S 34° 10' E 24° 42'	69	23.0	4.03	628	59	17	11	No

Underlined sites = Inland sites, Sites not underlined = Coastal sites; Sites in italics = south coast sites, Sites not in italics = west coast sites; Sites in bold = Eastern Cape site, Sites not in bold = Western Cape sites; De Martonne aridity index may be classified as follows: Arid, H<10; Semi-Arid, 10≤H≤20; Mediterranean, 20≤H≤24; Semi-Humid, 24≤H≤28; Humid, 28≤H≤35; Very Humid, 35≤H≤55; Extremely Humid, H≤55 (Baltas, 2007); Bailey's (1979) classification of WCP: Strong Winter, ≥81%; Winter, 61-80%; Even, 41-60%; Summer, 21-40%; Strong Summer ≤20%.

Generally De Matronnes aridity index (DMAI) increases along the west coast from Clanwilliam towards Cape Town, moving from arid, through semi arid then Mediterranean, to a semi-humid climate (Table 2.1). In general coastal sites when compared to inland sites, of similar longitude or latitude along the west and south coast, have higher DMAI values. Along the south coast the DMAI generally decrease and then increase again from Cape Town towards Port Elizabeth, moving from semi-humid to Mediterranean to semi-arid and then again to Mediterranean and finally to a semi-humid climate.

The summer aridity index (SAI) decreases along the west coast from north to south (Table 2.1). Along the south coast the SAI decrease from west to east. Sites along the west coast tend to have

higher SAIs when sites along the west coast and south coast are compared. In general coastal sites when compared to inland sites, of similar longitude along the west coast and latitude along the south coast, have higher SAI values.

The winter concentration of precipitation (WCP) of sites decreases from west to east with the west coast sites having larger values than the south coast sites (Table 2.1). Sites closer to the Cape Peninsula tend to have the highest WCP. All the sites are characterised by a winter rainfall regime except for Burgerspos being strong winter and Welgelegen being characterised by an even rainfall regime. When the moisture matrix of the SAI and winter concentration of precipitation of the sites are compared to the moisture matrix of the SAI and winter concentration of precipitation in Rutherford and Westfall (1986) all the sites except Rietvlei and Travellers Rest, which falls within the Succulent Karoo biome, fall within the Fynbos biome.

The soil texture composition of sites tends to be dominated by the sand fraction, especially for sites closer to the coast (Table 2.2). The sand fraction declines with distance from the coast. The soil of most sites can be classified according to soil texture as sand. The silt fraction tended to be the largest after the sand fraction with clay being the smallest.

Table 2.2:
The soil texture composition of the ten *A. saligna* study sites consisting of the sand fraction, silt fraction and clay fraction.

Site	Sand (%)	Silt (%)	Clay (%)	Soil classification
Travellers Rest	86	10	4	Sand
Rietvlei	98	0	2	Sand
Bossiesvlei	78	22	0	Loamy sand
Locheim	65	30	5	Sandy loam
Swartwater	93	6	1	Sand
Burgerspos	93	5	2	Sand
Buffelsrivier	90	5	5	Sand
Fairfield	88	9	3	Sand
Haasvlakte	89	10	1	Sand
Welgelegen	76	18	6	Loamy sand

Underlined sites = Inland sites, Sites not underlined = Coastal sites; Sites in italics = south coast sites, Sites not in italics = west coast sites; Sites in bold = Eastern Cape site, Sites not in bold = Western Cape sites.

2.3.2. Biological Factors

The average tree diameter of the *A. saligna* site situated in the Eastern Cape (Welgelegen) is larger than that of all the sites situated in the Western Cape (Table 2.3). *Acacia saligna* populations along the south coast have smaller average tree diameters, than sites along the west coast, except for the trees of Haasvlakte having a greater average tree diameter than the trees of Rietvlei.

Therefore, Haasvlakte and Rietvlei are the only west and south coast sites that are similar in terms of their average tree diameter. Consequently, as tree size is generally correlated with age for Port Jackson trees (Wood and Morris, 2007), the trees of the *A. saligna* stands along the west coast are assumed to be older than the trees of the south coast *A. saligna* stands. Rietvlei is the only site along the west coast that differs from the other sites along the west coast in terms of tree size. All other west coast sites are at least similar to one other west coast site in terms of tree size.

Table 2.3:
Average tree diameter (±SD), tree density, galls per tree and weevil damage for ten *A. saligna* sites.

Site	Tree diameter (mm)	Similarity	Tree density (ha^{-1})	Similarity	Galls per tree	Weevil damage (%)
Travellers Rest	84 ± 60	B	7 440 ± 7 682	B,C,D	63	0
Rietvlei	41 ± 30	E	57 040 ± 47 824	A	150	0.6
Bossiesvlei	61 ± 41	C,D	14 880 ± 12 494	B,C,D	54	0
Locheim	59 ± 20	B,C	3 920 ± 2 105	D	39	0
Swartwater	60 ± 38	C,D	7 440 ± 5 174	B,C,D	42	0.3
Burgerspos	49 ± 27	D	17 840 ± 7 635	A,B	27	42.1
Buffelsrivier	22 ± 14	G	19 760 ± 17 955	A,B	NA	NA
Fairfield	35 ± 41	F	14 160 ± 5 189	B,C	73	2.3
Haasvlakte	48 ± 42	E	11 360 ± 8 336	B,C,D	80	0
Welgelegen	84 ± 35	A	4 640 ± 1 403	C,D	163	0

Underlined sites = Inland sites, Sites not underlined = Coastal sites; Sites in italics = south coast sites, Sites not in italics = west coast sites; Sites in bold = Eastern Cape site, Sites not in bold = Western Cape sites; NA indicates data not available; The similarity columns indicates the results of the Anova and multiple comparison of mean test for the Colum on its left hand side. The Anova test compares sites to one another showing which sites are similar or different from each other in this respect.

The Western Cape Port Jackson populations all have greater tree densities than the Eastern Cape stand (Table 2.3). Although there are differences in the tree densities of the sites along the south coast, these differences are not significant. The same is true for the sites along the west coast with the exception of Rietvlei and Locheim being significantly different from the other west coast sites as well as from each other in terms of tree density. Rietvlei and Locheim are the sites with the highest and lowest tree densities respectively. When west coast *A. saligna* stands are compared to south coast stands, Rietvlei and Locheim are also the only Port Jackson stands that are different in terms of their tree densities. Tree density is generally larger at sites which experienced recent fires and declines with years from the fire event (Table 2.4).

There is a tendency for *A. saligna* stand tree densities to decline with an increase in tree size; leading to *A. saligna* stands with higher tree diameters having lower tree densities than sites with lower tree diameters (Figure 2.3). The relationship between tree density and tree diameter is not significant as indicated by the Pearsons correlation coefficient.

Table 2.4:
Site history in terms of invasion history, stand age and time since last fire (years) for the ten *A. saligna* study sites.

Site	Invasion History	Stand Age	Time Since Last Fire
Travellers Rest	30+	10+	10
Rietvlei	23+	22+	3
Bossiesvlei	80+	10+	NA
Locheim	80+	15	12
Swartwater	23+	16+	12
Burgerspos	23+	18+	16
Buffelsrivier	24+	2.5+	NB
Fairfield	12+	12+	NA
Haasvlakte	64+	10+	10
Welgelegen	23	23	NB

Underlined sites = Inland sites, Sites not underlined = Coastal sites; Sites in italics = south coast sites, Sites not in italics = west coast sites; Sites in bold = Eastern Cape site, Sites not in bold = Western Cape sites; + indicates that value may be large with associated number being the minimum value for the estimation; NA indicates data not available; NB indicated that the stand has never been burnt; Buffelsrivier is mechanically cleared every 3 years.

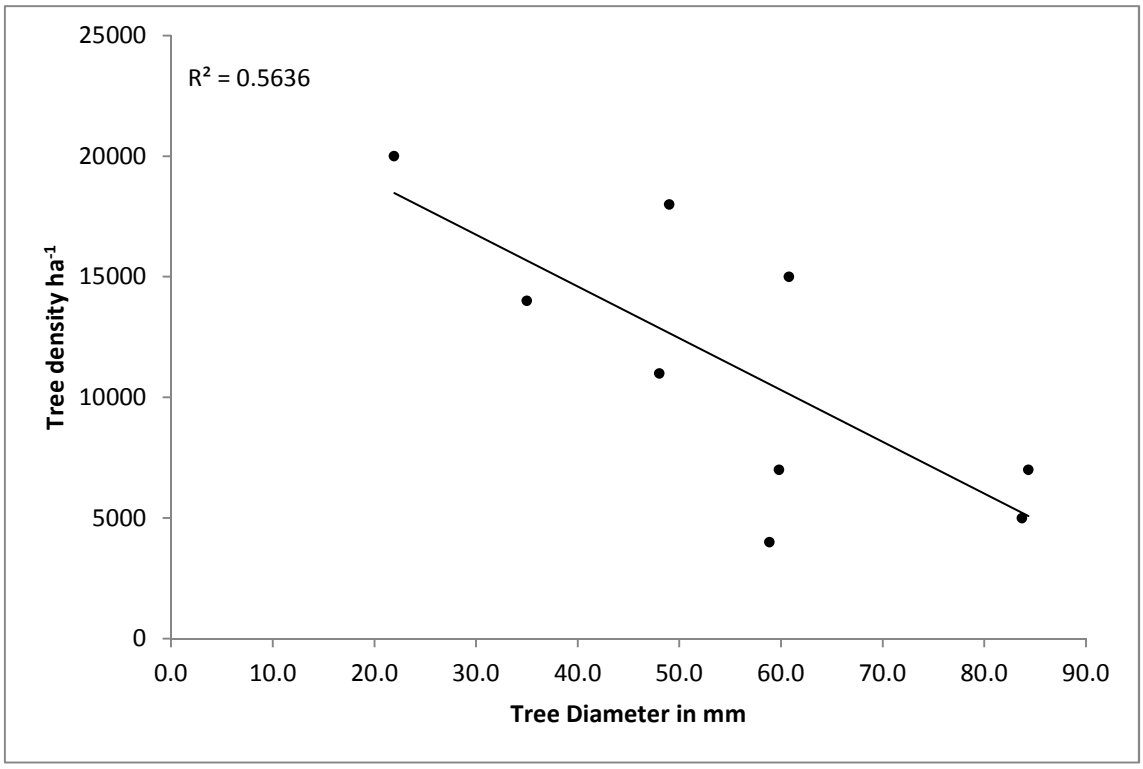

Figure 2.3: The average tree density of *A. saligna* plotted against the average tree diameter for nine *A. saligna* sites. (Pearsons correlation coefficient = -0.75).

The west coast sites have an increased average number of galls per tree with an increase in the tree diameter, with the exception of Rietvlei (Table 2.3). The same pattern occurs along the south

coast where populations with larger trees had greater average gall rust numbers per tree (as would be expected). However on average, there were more galls per tree in the south coast populations, even though they were, on average, smaller than the west coast trees.

Melanterius compactus damage was present at all the sites where this biological control agent has been released (F.A.C. Impson personal communication) (Table 2.3). The weevils were released after 2004 at these sites (Impson *et al*., 2011). In addition to the three sites where they had been released there was one extra site that incurred seed damage by seed feeding insects. This site is situated at a considerable distance from the other sites along the west coast where *M. compactus* has been released. Native weevils were found in the traps at these sites. The weevils could not be identified but they were not *M. compactus* (confirmed by experts). The emergence holes in the pod capsules were also larger than the emergence holes in *M. compactus* damaged capsules from sites where this weevil was present. The only site where there was weevil damage of note was at Burgerspos (42.2%). No published data exists to which the damage levels of the weevil could be compared, as the weevil is only described in the literature as having damage levels of 90 % (Impson *et al*., 2011). However, it is reasonable to assume that the estimated damage levels were accurate, as the pod capsule estimates minus the estimated damage levels of the weevil are in the same order of magnitude as the estimated seed rain of the sites where the weevils were present.

According to the above-described results the following predictions about *A. saligna* seed production can be made:

- Based on the climatic and edaphic parameters of the study and the findings of previous studies (Milton, 1980; Goal and Fox, 2002; Zegada-Lizarazu *et al*., 2007), seed production of *A. saligna* populations should generally increase along the west coast from Clanwilliam towards Cape Town and further from Cape Town towards Port Elizabeth, being larger nearer to the coast along this gradient.
- According to tree size, seed production should generally be larger along the west coast than along the south coast when sites in the Western Cape are compared.
- The Eastern Cape site should have the largest seed production according to tree size. However, the Eastern Cape site should also have the lowest seed production according to the gall rust fungus estimates.
- The Western Cape sites should have smaller seed production along the south coast than along the west coast when gall rust estimates are compared.

2.3.3. Seed production of the Western Cape sites

The south coast Port Jackson sites have higher pod capsule rain and seed rain than the west coast inland sites (the latter with larger and older trees in general, (Table 2.3), when sites not situated along watercourses are compared (Table 2.5). The values of seed rain and pod capsule rain of these sites are also significantly different. Bossiesvlei and Locheim experience more arid conditions as they have higher SAI values, lower DMAI values (Table 2.1) and finer textured soil composition (Table 2.2) than Buffelsrivier and Haasvlakte.

When coastal sites along the south coast are compared to coastal sites along the west coast, not situated along watercourses, only the seed rain of Swartwater is significantly larger than that of the south coast sites (Table 2.5). Swartwater and Burgerspos are also characterised by larger trees (Table 2.3) and SAI's values (Table 2.1) than Buffelsrivier and Haasvlakte. Swartwater and Burgerspos also have soils with a slightly coarser texture (Table 2.2). Although the seed rain of Burgerspos is significantly smaller than that of Buffelsrivier and Haasvlakte, it is also the site which had the largest percentage weevil damage (Table 2.3). This is also reflected in the seed rain of Burgerspos being approximately a third of its pod capsule rain.

Table 2.5:
The average (± SD) seed rain and pod rain for ten sites across the distribution of *A. saligna* in South Africa.

Site	Seed rain (m^{-2})	Similarity	Pod rain (m^{-2})	Similarity
Travellers Rest*	13 627 ± 7 361	A	10 546 ± 7 335	A
Rietvlei*	11 576 ± 5 707	A	10 130 ± 4 573	A
Bossiesvlei	1 409 ± 756	D,E	1 936 ± 1 169	D
Locheim	1 039 ± 724	F	1 150 ± 965	E
Swartwater	6 167 ± 3 767	B	5 063 ± 3 045	B
Burgerspos	975 ± 526	E,F	2 679 ± 1 314	C,D
Buffelsrivier	2 735 ± 1 702	C	NA	NA
*Fairfield**	1 866 ± 1 095	C,D	2 568 ± 1 678	C,D
Haasvlakte	2 324 ± 1 024	C	3 368 ± 2 050	B,C
Welgelegen	286 ± 404	G	346 ± 460	F

Underlined sites = Inland sites, Sites not underlined = Coastal sites; Sites in italics = south coast sites, Sites not in italics = west coast sites; Sites in bold = Eastern Cape site, Sites not in bold = Western Cape sites; * indicates sites situated along watercourses; NA indicates data not available; The similarity columns indicate the results of the Anova and multiple comparison of mean test for the Column on their left hand side. The Anova test compares sites to one another showing which sites are similar or different from each other in this respect.

Pod capsule rain and seed rain for the west coast coastal site, Swartwater, are significantly higher than that of the west coast inland Port Jackson sites (Table 2.5). The west coast inland sites also have trees that are of similar size to that of Swartwater. Both the SAI and the DMAI of the inland

sites are lower than that of Swartwater (Table 2.4) and they have soil with a finer texture (Table 2.5). The other west coast coastal site Burgerspos, which has smaller trees, is similar to the west coast inland sites in regards to its seed rain but has a higher pod capsule count than both sites. However, Burgerspos also has the highest percentage damage done to its seeds by *M. compactus* (Table 2.3). Locheim and Bossiesvlei have a higher SAI than that of Burgerspos, a lower DMAI and a finer soil texture and *M. compactus* is absent at these sites.

The south coast inland *A. saligna* site, Fairfield, has larger pod capsule rain and seed rain estimates compared to all the sites along the west coast except for Swartwater and the other two Port Jackson stands situated along watercourses (Table 2.5). Furthermore, Fairfield's average tree size and SAI is smaller than that of all the sites along west coast (Table 2.3). Fairfield has a coarser textured soil than the west coast inland sites but a finer textured soil when compared to the coastal sites (Table 2.2).

When compared to the south coast Port Jackson sites in the Western Cape, Fairfield has the smallest seed production estimates (Table 2.5). However, all the seed production estimates of the south coast sites are not significantly different from each other. Furthermore Fairfield's *A. saligna* trees are significantly smaller in size than that of Haasvlakte but are significantly larger than the trees of Buffelsrivier (Table 2.3). Fairfield also has the smallest SAI and DMAI (Table 2.1) and finest soil texture (Table 2.2) of the south coast sites in the Western Cape.

The *A. saligna* stand situated at Travellers Rest is larger in terms of its seed production when compared to the *A. saligna* stand at Rietvlei, although these two sites are not significantly different in this respect (Table 2.5). These two Port Jackson stands are both situated along watercourses and when compared to the other *A. saligna* sites they both have larger seed rain and pod count estimates. Rietvlei and Travellers Rest are also significantly different in respect of their seed production estimates to the other sites. Rietvlei and Travellers Rest have the lowest DMAI and highest SAI values of all the sites (Table 2.1). Travellers Rest experience more arid conditions throughout the year than Rietvlei and also has a finer soil texture (Table 2.2).

According to the comparisons done above, *A. saligna* populations in the Western Cape will produce more seed in riparian habitats than in non-riparian habitats. Riparian *A. saligna* populations will produce more seed with an increase in the SAI. The seed production of non-riparian *A. saligna* populations will increase with a decrease in the summer aridity index, an increase in the sand fraction and with closer proximity to the coast. Older *A. saligna* populations will produce more seed when populations under similar climatic conditions and moisture regimes (riparian or non-riparian populations) are compared.

2.3.4. Seed production of the Eastern Cape site

Lastly, the Eastern Cape site, Welgelegen, has the smallest values for both pod capsule rain and seed rain m^{-2} (Table 2.5) and is significantly different from all the other sites in this respect. Welgelegen is the site that has the largest trees and number of galls per tree (Table 2.3), smallest SAI and is the only site that is not characterised by a winter rainfall regime (Table 2.1) and which receives precipitation throughout the year. Welgelegen also has the finest soil texture (Table 2.2) after Locheim and also has never been burnt (Table 2.4).

The prediction for the seed production according to climate and soil was confirmed except for the Eastern Cape site. The prediction for tree size was not supported. The effect of tree size only becomes apparent when *A. saligna* populations with similar moisture regimes (SAI, DMAI) are compared. When *A. saligna* populations of similar moisture regimes are compared larger trees generally produce more seed, with the Eastern Cape site being the exception. The effect of the gall rust fungus is not apparent through the gall rust estimates in the Western Cape sites. The Eastern Cape site had the smallest seed production as predicted by the gall rust fungus infection.

2.4. Discussion

According to the results described above, abiotic parameters have the largest influence on seed production. Available moisture during times of high evapotranspiration is important for seed production. Seed production is the lowest in more drought stressed areas and increases with an increase in the rainfall received during the hot summer months. However, sites situated along watercourses are an exception to this pattern. *A. saligna* populations along watercourses produce more seed under more arid conditions. Therefore, in this situation more constant warm temperatures will lead to higher seed production. Well defined winter conditions also seem to be important for seed production. When areas with similar abiotic conditions are compared it becomes apparent that seed production is larger in stands characterised by older trees.

2.4.1. Site conditions of *A. saligna* populations in South Africa

Acacia saligna populations studied during this work in South Africa occur in similar climatic and soil conditions as *A. saligna* populations in south-western Australia (Cronk and Fuller, 1995; Marcar *et al.*, 1995; O'Sullivan *et al.*, 2009). Travellers Rest was the only site that deviated from this observation, occurring in an area receiving slightly less precipitation (by 5 mm) than *A. saligna* populations in their native range. This is also one of two Port Jackson populations situated in the

succulent Karoo biome. However, both Travellers Rest and Rietvlei, the succulent Karoo Biome *A. saligna* populations, are situated along watercourses and in its native range Port Jackson is frequently situated in riparian habitats were the annual precipitation is low (O'Sullivan *et al*., 2009). Cronk and Fuller, (1995) also described *A. saligna* populations in more arid environments in South Africa to be restricted to streams and rivers. *Acacia saligna* populations along watercourses therefore have access to more water than rainfall alone (O'Sullivan *et al*., 2009). Furthermore in Chile it has been recorded that *A. saligna* is able to survive in situations where the annual precipitation is less than 100 mm (O'Sullivan *et al*., 2009). However, in such circumstances proximity to the coast and maritime mists are described as an important addition to rainfall (O'Sullivan *et al*., 2009).

2.4.2. Reproductive output

Most seed was produced by *A. saligna* populations along watercourses, followed by sites which receive more rainfall during the summer months in South Africa. The seed production of *A. saligna* populations in the study appears to be closely linked to water availability during summer months with reproductive ouput being higher when water is more readily availabile during this time of the year. Goal and Fox (2002) had similar findings in Australia with *A. saligna* producing more seed during wet years when compared to dry years.

Milton (1980) described two situations of water availability influencing the growth of *A. saligna* namely run-off and run-on. Run-on situations (sites along watercourses, dams etc.) are only limited by temperature with the growing season ending with the onset of winter. Run-off situations are limited by water with the growth season ending when it becomes limiting. Consequently the growth rate of *A. saligna* will be higher in areas where water is more readily available throughout the year (Milton, 1980; Zegada-Lizarazu *et al*., 2007).

The seed production of *A. saligna* populations in this study tends to have the same pattern as described for its growth rate under different moisture regimes. The effect of water availability on reproduction is consequently indirect through its effect on growth. The growth rate of *A. saligna* will influence the reproduction of *A. saligna* individuals through:

- Determining the amount of carbohydrates produced and stored and consequently the resources available for allocation to reproduction within and between seasons (Gaol and Fox, 2002; Zegada-Lizarazu *et al*., 2007).
- Affecting the number of new shoots that are available for the formation of reproductive structures within a season (Gaol and Fox, 2002).

Larger reproductive effort as a consequence of greater water availability has also been assessed in other semi-arid environments as well as under other climatic regimes (Matlack and Good, 1990; Gutiérrez *et al*., 2000; Bossuyt and Hermy, 2001; Stark *et al*., 2008; Caballero *et al*., 2008; Li *et al*., 2011).

2.4.3. Influence of proximity to the coast, soil texture and DMAI on seed production.

Coastal Port Jackson stands tend to produce more seed than inland stands. This may be as a consequence of coastal sites having higher DMAI and coarser soil textures. Higher DMAI may indicate sites that have greater water availability at the beginning of the growing season. Therefore, the available water will decline more slowly in areas with larger DMAI and will lead to faster growth and longer growing seasons (Zegada-Lizarazu *et al*., 2007), leading to higher reproductive output. Coarser textured soil will allow for faster water infiltration, storage of water deeper down in the soil and it will lose less water to the atmosphere as a consequence of evapotranspiration (Fravolini *et al*., 2005), resulting in more water being available during the dry summer months for *A. saligna* trees which will lead to greater growth rates and reproduction. *Acacia saligna* populations close to the coast may also receive water through maritime mist which will increase the water that is available to the plant during the hot summer months which will lead to greater reproductive output (O'Sullivan *et al*., 2009).

2.4.4. The effect of *U. tepperianum* on the reproductive output of *A. saligna*.

The higher gall rust fungus estimates in the south coast *A. saligna* populations than in the west coast populations may indicate that infection takes place at a faster rate in more moist climates. The importance of moisture for the infection of young growth and reproductive structures by *U. tepperianum* is illustrated by lab experiments (Morris, 1987). Plants are inoculated with teliospores of *U. tepperianum* in a water suspension. Afterwards inoculated plants are also covered with plastic bags (Morris, 1987). Detached *A. saligna* leaflets that were inoculated were also placed on moist filter paper in petri dishes which were then incubated to be inspected for infection afterwards (Morris, 1987). Successful infection might also be influenced by temperatures during growth period as favourable temperatures for gall rust fungus infection is between 18 and 26 ˚C (Morris, 1987).

Reproduction of *A. saligna* is directly reduced by *U. tepperianum* through the infection of newly formed reproductive structures and indirectly through the infection of newly produced growth structures (Morris, 1987; 1991). The number of galls on an *A. saligna* tree through time is a function of the infection rate of newly produced growth and reproductive tissue over time and the number of infected growth and reproductive structures that are abscised or lost to other factors e.g. wind damage within a season. The effect of the gall rust fungus over time depends on the build up of galls on the tree, whether the galls are annual or perennial and on the climatic conditions of the location. *Uromycladium tepperianum* reduces the growth rate of *A. saligna* through reducing the number of photosynthetic structures as well as using resources of its host through time, which would otherwise be allocated to maintenance, growth and reproduction.

Uromycladium tepperianum infection is possibly faster over time under more moist conditions as *A. saligna* individuals grow faster under these circumstances leading to more young growth and reproductive structures being available for infection. Furthermore, infection rate also seems to be higher in situations where more water is received through precipitation during periods of growth, and maritime mist, with water being important for infection. Therefore, the direct effect of *U. tepperianum* should be the greatest in situations where water is more readily available and where water is received during periods of growth through precipitation and maritime mist. However, as *A. saligna* populations have more resources to allocate in more moist conditions the indirect effect of *U. tepperianum* will be smaller when compared to more arid environments. The indirect effect on *A. saligna* trees will depend on the number of new growth that the fungus can infect, conditions favouring infection, the rate of build up over time and the resources (e.g. water) that are available to the host tree. Under conditions where water is available throughout the year *A. saligna* trees might rather die from old age. However, the fungus will have reduced the life-time fecundity of the *A. saligna* tree.

The indirect effect of *U. tepperianum* will be the largest under more arid conditions. This will result in even slower growth and ultimately the faster death of *A. saligna* trees in arid environments. Although the effect of the gall rust fungus is not readily apparent in the Western Cape this is probably the cause of stands being a mixture of low and heavily infected trees. In conclusion, the effectiveness of *U. tepperianum* to reduce the reproductive output of *A. saligna* will depend on the total moisture available throughout the year as well as rainfall and mist events during periods of growth including other conditions influencing the rate of infection (stand density etc.).

2.4.5. The effect of *Melanterius compactus* on reproductive output of *A. saligna*

The reason for the low impact of *M. compactus* on the seed production of *A. saligna* at the sites where it had been released may be ascribed to the weevil populations having established recently and to their slow dispersal rates from points of release or establishment. The slow dispersal rate of *M. compactus* is illustrated by the species being absent at Haasvlakte, a site between release sites at Bredasdorp and Struisbaai where the weevil was released in 2003 (Impson *et al*., 2011). The percentage of weevil damage should increase over time. However, the effectiveness of the weevil as a biological control agent will depend on its ability to consistently have damage levels of close to 100 % on the seed production of every tree within the population within a season and over seasons and the rate at which these damage levels are reached once the weevils have been released into the *A. saligna* populations. Damage levels of close to 100 % are required to translate into a significant reduction in the number of seed in the soil. Such high damgage levels will be required as the size of seed production of Port Jackson populations of different ages and under different environmental conditions will vary, as can be seen in the seed production size of the *A. saligna* populations in the study. For instance 1 % (which implies weevil damage levels of 99 %) of Travellers rest seed production (136 seeds m^{-2}) is 45 times the size of 1 % of Welgelegens seed production (3 seeds m^{-2}). Furthermore 10 % (which implies weevil damage levels of 90 %) of Travellers Rest seed production (1 363 seeds m^{-2}) is larger than and similar to the seed production of many of the other sites (Locheim, Bossiesvlei, Burgerspos and Welgelegen) underwhich considerable seed banks have accumulated (see Chapter 3). The consistency in the damage levels will be required to reduced the seed in the soil not only under individual trees but under the whole *A. saligna* stand and to translate not only into a reduction in the number of seed in the soil but to reduce the seed in the soil to such a level as to cause a decrease in the number of seedlings that will germinate. Milton (1980) estimated that 2.3% of the freshly fallen seeds of *A. saligna* are able to germinate without prior heat treatment. This small percentage of seed that are able to germinate immediately was enough to lead to the establishment and spread of *A. saligna* across its distribution range in South Africa. Consequently weevil damage levels will need to be higher than 97.7 % to lead to a reduction in the number of seed in the seed bank and to reduce the dispersal rate of the tree. Furthermore, the environmental tolerances of the weevil over the distribution range of *A. saligna* in South Africa and the ability of weevil populations to persist and recover after fire events will also be essential in determining their success.

2.4.6. The Eastern Cape site Welgelegen

The low reproductive output at Welgelegen may be attributed to high gall rust infection, rain damage, senescence, soil texture and grass cover. The average number of galls per tree should be high under these conditions as the trees will grow fast and the moist conditions should favour infection. Therefore the direct loss of reproductive structures, as a consequence of gall rust infection, under these conditions should be high resulting in low reproductive output. This site also has never been burnt and is possibly a good example of how the gall rust fungus reduces the seed production of *A. saligna* over time. The flowers lost due to rain damage may also be the highest in this situation. It might also be that the trees are producing small number of seed as a consequence of senescence. Another reason may be that as a consequence of its finer soil texture, more water is stored in the upper soil layers and that the grass that is present underneath its canopy further decrease the available water leading to smaller reproductive output.

2.4.7. Dispersal of *A. saligna* seed

A large proportion of the seeds, fall with the seed pods to the ground or pods and seed fall in a similar pattern towards the earth. This will possibly lead to seeds being more aggregated on the soil surface. Furthermore the pods are buoyant allowing for the easier dispersal of seed along watercourses and the soil surface when it rains.

2.4.8. Management implications

2.4.8.1. Non-Riparian *A. saligna* populations

The seed production should increase from Clanwilliam towards Cape Town and further along the south coast towards Bredasdorp, being larger nearer to the coast, when non-riparian *A. saligna* populations of similar age are compared. Therefore, the threat of seed banks should increase in a similar pattern along this gradient. When sites under similar abiotic conditions are compared, older *A. saligna* populations are likely to produce more seed.

Whether the seed production increases or decreases from Bredasdorp further along the south coast is not apparent as seed production was only estimated at one site in the Eastern Cape. It may therefore be that this site is not representative of the *A. saligna* populations in the Eastern Cape. The reason for the lack of sampling sites between Bredasdorp and Oesterbay is due to

A. saligna decreasing in dominance with no populations occurring, at least along the main roads, that are monospecific and larger in extent than one hectare.

2.4.8.2. Riparian *A. saligna* populations

Seed production of riparian *A. saligna* populations should increase from Bredasdorp towards Cape Town and further from Cape Town towards Clanwilliam, with sites near the coast producing more seed. When sites under similar abiotic conditions are compared, older riparian *A. saligna* populations should produce more seed. Riparian *A. saligna* populations should produce more seed than non-riparian populations.

2.4.8.3 Prioritization recommendations

According to the size of seed production and the rate that it will increase with time alone clearing could be prioritized as follows:

1. Old riparian *A. saligna* populations, with stands in more arid environments having first priority
2. Young riparian *A. saligna* populations, with stands in more arid environments having first priority
3. Old non-riparian *A. saligna* populations, with stands in more moist environments having first priority
4. Young non-riparian *A. saligna* populations, with stands in more moist environments having first priority.

Riparian *A. saligna* populations should also have priority as the dispersal distances of their propagules and the rate at which they spread will be greater than that of non-riparian populations. The rate at which the seed bank accumulates over its distribution range should follow the same pattern as the seed production and consequently clearing programmes targeting the seed bank may be prioritized in a similar manner.

2.5. Conclusion

The seed production over the distribution of *A. saligna* remains large. The number of seed produced by *A. saligna* populations is primarily affected by moisture availability, with more seed being produced in areas where moisture is more readily available. The effect of a lack of moisture is amplified by the gall rust fungus leading to even lower seed production in these areas. Over the distribution of *A. saligna*, *U. tepperianum* appears to be the most effective of the two biological control agents in reducing the seed production of *A. saligna*. However, the seed production of *A. saligna* is still too high in the presence of these control agents to translate into a reduction in the seed bank and consequently active management will be required to effectively remove *A. saligna* from areas where it has invaded.

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Chapter 3: Invasive *Acacia saligna* seed banks in South Africa: A spatial assessment in the context of environmental variation

Abstract

In South Africa, various Australian *Acacia* species have become invasive, some of which have been present for the past two centuries. Invasive success and resistance to eradication of many alien Acacias can be ascribed to their persistent soil stored seed banks. *Acacia saligna* is the most troublesome in this respect, accumulating large seed banks in relatively short time periods. Although there have been a few site-specific studies assessing the size of the seed bank of *A. saligna,* an assessment of the seed bank over its entire invaded range is lacking. Furthermore the influence of environmental factors on the seed bank is poorly understood. Information in this regard has been highlighted as essential for development of tools and strategies to achieve invasion control. This study aimed to fill this gap through assessing the seed bank and the influence of different environmental factors over the distribution range of Port Jackson in South Africa. The study assessed the seed bank of *A. saligna* to be large over its distribution range. The age of the *A. saligna* stand, the amount of water available during the dry summer months, a well defined winter in terms of temperature and soil texture were assessed to be important for determining where *A. saligna* seed bank accumulation rates will be the largest. Riparian and non-riparian conditions were identified as being important to quantify in order to accurately predict seed bank size. In non-riparian *A. saligna* populations the seed bank increases along the west coast from Clanwilliam towards Cape Town and further from Cape Town towards Port Elizabeth with the opposite being true for Riparian populations.

Key words: Invasive alien plant, geographical gradient, seed, abiotic, biotic

3.1. Introduction

The ability of many Australian Acacias to accumulate and maintain persistent seed banks prevents their effective and sustainable removal (Holmes *et al*., 1987; Esler and Boucher, 2004; Richardson and Kluge, 2008; Gibson *et al*., 2011; Wilson *et al*., 2011). Seed banks absorb the effect of disturbance (e.g. fire, floods etc.) on population dynamics in the short-term through spreading risk and diminishing irregular fluctuations (Harper 1977; Louda, 1989, Caballero *et al*., 2005; Caballero *et al*., 2008b). Seed banks create the opportunity for Australian *Acacia* populations to persist in

time and space and to re-establish in the future in an environment that may temporarily be free from biological control agents and management (Strydom *et al*., 2012).

The accumulation of persistent seed banks can be attributed to Australian Acacias having pioneer characteristics (e.g. rapid growth, early reproduction, production of many small seed, etc.) as well as being adapted to periodic fires events (Bell *et al*., 1993). The adaptation to fire is due to seed being enclosed by a water impermeable testa (Milton and Hall, 1981) which imposes dormancy until a heat pulse adequately damages it, allowing water imbibition and consequent germination (Milton and Hall, 1981; Tran and Cavanagh, 1984; Jeffery *et al*., 1988). Most Australian *Acacia* seed in the seed bank are viable (85 %) (Milton and Hall, 1981) and are able to remain so for 50 or more years (Holmes, 1989). The lowest and highest seed bank densities recorded for invasive Australian Acacias have been measured to be 1 430 m^{-2} (*A. cyclops*) and 212 000 m^{-2} (*A. saligna*) respectively (Holmes, 1987; Morris, 1997). Therefore, *A. saligna* (Port Jackson) in terms of its seed bank poses the greatest threat to management efforts of all the Australian Acacias.

Acacia saligna is a small leguminous shrub or tree (Morris, 1991; Henderson, 2001) indigenous to south-western Australia (Milton and Hall, 1981; O'Sullivan *et al*., 2009) which is thought to have been introduced into South Africa for the first time in 1838 (Shaugnessy, 1978). In the mid 1980s *A. saligna* was assessed to be potentially the most damaging invasive species in the coastal lowlands of the south-western Cape (Macdonald and Jarman, 1984; Van Wilgen and Richardson, 1985). After 25 years Port Jackson was rated as second of the 20 most prominent invaders in the fynbos biome (Henderson, 2007). In the western, southern and eastern Cape coastal regions *A. saligna* has formed large dense stands over a vast area on conservation, water catchment and agricultural land (Richardson *et al*., 1992; Morris, 1997; Morris, 1999). This has resulted in the replacement of natural vegetation, alterations in ecosystem processes and interference with agricultural practices (Richardson *et al*., 1992; Morris, 1997; Morris, 1999). Therefore Port Jackson has become part of the focus of alien vegetation removal programs.

Mechanical and chemical control is associated with high costs and consequently is only feasible in valuable conservation and intensively farmed areas (Morris, 1991). Where *A. saligna* occurs there are few areas where these populations are actively being managed (Morris, 1991). Consequently, two biological control agents, *Uromycladium tepperianum* (gall rust fungus) and *Melanterius compactus* (seed feeding weevil), have been introduced to reduce seed production and better control the invasion. *Uromycladium tepperianum* has been present in South Africa for the past 30 years. Furthermore the gall inducing rust fungus attacks young expanding phyllodes, stems and reproductive tissue and has decreased stand density (to 5 – 10 % of the original tree density) (Morris, 1999), reduced canopy cover and seed production (Wood and Morris, 2007). In South Africa *Melanterius compactus* has been released in 18 sites, 3 in 2001, 2 in 2003 and 13 since 2004 (Impson *et al*., 2011). The seed feeding weevil attacks developing seed pods and is

described as having damage levels of 90 % regularly (Impson *et al*., 2011). However, the seed bank remains large in the presence of these two biological control agents.

The annual increase in *A. saligna* population seed banks is a result of stand age, stand density, (Richardson and Kluge, 2008), predation, decay, germination (Weaver and Cavers, 1979; Milton and Hall, 1981), substrate type and degree of soil disturbance (Holmes and Cowling, 1997). However, *A. saligna* seed banks are primarily the consequence of its seed production and ability of its seed to remain dormant for long time periods. Wet winter conditions are needed to induce flowering and precipitation is essential after flowering to encourage pod development and good seed set (Gaol and Fox, 2002). *Acacia saligna* is able to reproduce within 2 years after germination, but only produce large seed crops after 5 years (Milton and Hall, 1981). The ability to reproduce within a few years from germination has been assessed to be crucial for the invasion success of Australian Acacias (Gibson *et al*., 2011). Port Jackson trees flower with the onset of spring (August to September) (Milton, 1980) and less than 1 % of flowers produce mature pods (Milton and Hall, 1981). Pods reach maturity in early summer (December) after which they dehisce and release their seed and all pods are shed by late summer (February/March) (Milton, 1980). Seeds fall straight to the ground resulting in seed densities being the greatest close to the parent plant and declining with distance from it (Milton and Hall, 1981). As Port Jackson populations mature, the annual seed bank input will be larger and will tend to stabilize when trees reach an age of 30 years (Milton and Hall, 1981). Before *U. tepperianum* was released in South Africa, seed in the canopy was estimated to be 10 562 m^{-2} and seed rain to be 5 443 m^{-2} for mature trees and 530 m^{-2} for saplings (Milton and Hall, 1981). The seed rain has since been recorded to be between 2 645 m^{-2} and 13 472 m^{-2} for four sites in 1989 (Wood and Morris, 2007), 2 102 m^{-2} for one site in 1990 (Holmes, 1990a; Holmes, 1990b) and between 446 m^{-2} and 3035 m^{-2} for four sites in 2004 (Wood and Morris, 2007); there is therefore some indication that biological control has reduced seed output, although this has not been at the levels required to translate into a marked reduction of seed in the seed bank. Furthermore, it should be noted that these estimations were made under stands of different ages and environmental conditions.

Spatially and with time seed production and consequently seed bank size and accumulation rate will also be determined by the growth rate of *A. saligna.* Growth rate will influence the reproduction of *A. saligna* individuals through determining the amount of carbohydrates produced and stored and consequently the resources available for allocation to reproduction within and between seasons (Gaol and Fox, 2002; Zegada-Lizarazu *et al*., 2007) and by affecting the number of new shoots that are available for the formation of reproductive structures within a season (Gaol and Fox, 2002). The growth rate of *A. saligna* will vary over time and space as a consequence of water availability and temperature (Milton, 1980). The growth season will be shorter in locations where water becomes limiting earlier during the hot summer months (Milton, 1980). In situations where water is not limiting (e.g. watercourses) temperature will determine the end of the growth season

(Milton, 1980). Riparian *A. saligna* populations should therefore have longer growing seasons and their trees should increase faster in size with time when compared to non-riparian populations. *Acacia saligna* should follow the same reproductive pattern producing more seed under conditions where water is more readily available throughout the year.

In addition to having an understanding of the reproductive potential of *A. saligna*, the spatial distribution of the seed bank is essential as this will influence its population dynamics e.g. determine whether seed will survive a fire event (Tozer, 1998). Furthermore the spatial distribution of the seed bank will also influence the accuracy of sampling methods and consequently study results (Strydom *et al*., 2012). In general, source individuals mainly determine spatial distribution patterns with the origin point, seed crop size, timing of seed release, dispersibility of seed (weight, plumes etc.), distributing agent activity (wind direction and velocity) and fluctuations in environmental conditions all playing a role during dispersal (Harper, 1977; Leck, 1989). Once seed are on the soil surface they may be subjected to movement along the surface by wind or water until they are caught by obstacles or fall down crevices (Harper, 1977). Animals and insects may also disperse seed or bury them (Harper, 1977; Holmes, 1990a; Midgley and Bond, 1995; French and Major, 2001). The horizontal distribution of the seed bank of *A. saligna* in South Africa is clumped (Strydom *et al*., 2012), a pattern which is a result of seed burial by ants (Milton and Hall, 1981; Holmes, 1990a; Holmes, 1990b) or of trees having a clumped distribution pattern (Milton and Hall, 1981; Holmes *et al*., 1987; Benoit *et al*., 1992; Strydom *et al*., 2012).

The movement of seed into the soil is influenced by dispersal vectors (e.g. ants and water), soil organisms (e.g. mole rats), substrate type (Milton and Hall, 1981), percolation of water and openings left in the soil for example by decomposing roots (Harper, 1977). The largest proportion of *A. saligna's* seed bank is situated below the litter but within the upper 10 cm of the soil (Strydom *et al*., 2012). The number of seed in the soil decreases with depth (Milton and Hall, 1981; Tozer, 1998; Holmes, 2002; Strydom *et al*., 2012). The nature of the soil will determine how deep seeds will penetrate into the substrate (Milton and Hall, 1981; Richardson and Kluge, 2008), with seeds having been located at a depth of 35 cm in loose sandy soil (Milton and Hall, 1981; Strydom *et al*., 2012) and 80 cm in riparian soils (Esler and Boucher, 2004). After germination requirements have been met, seeds deeper in the soil profile germinate faster than seeds near the soil surface (Milton and Hall, 1981). However, seedlings of seeds situated near the surface are more vigorous than seedlings of seeds situated deeper in the soil profile during germination (Milton and Hall, 1981).

Many research papers have focused on *A. saligna* as a subject species, covering topics such as its invasion history (Roux, 1961), phenology (Milton and Moll, 1982, Jeffery *et al*., 1988, Zigada-Lizarazu *et al*., 2007; O'Sullivan et al., 2009), seed bank dynamics (Milton and Hall, 1981; Holmes *et al*., 1987; Holmes, 1988; Holmes, 1989; Holmes, 1990a; Holmes, 1990b; Tozer, 1998; Holmes, 2002; Gaol and Fox, 2002; George *et al*., 2008; Richardson and Kluge, 2008), biological control

and management (Milton and Moll, 1982; Holmes et al., 1987; Morris, 1987; Morris, 1991; Higgins *et al*., 1997; Morris, 1997, Morris, 1999; Impson *et al*., 2004; Wood and Morris, 2007, Impson *et al*., 2011), its effect on fire (Van Wilgen and Richardson, 1985), its effect on native ecosystems and biodiversity (Witkowski, 1991a; Witkowski, 1991b, Musil, 1993; Stock *et al*., 1995; Holmes and Cowling, 1997a; Holmes and Cowling, 1997b, French and Major, 2001, Holmes, 2002, Yelenik *et al*., 2004) and genetics (Millar *et al*., 2011). However, this is the first study attempting to determine the number of seed in the litter and soil over the entire invaded distribution range of *A. saligna* in South Africa. This is also the first attempt to sample the seed bank of an Australian *Acacia* over such a large distribution and environmental gradient. Although many biological factors affecting the seed bank dynamics of *A. saligna* have been studied, the effect of climatic and soil conditions on seed bank dynamics have largely been ignored. The study aimed to answer the following two questions:

1) What is the status of the seed in the seed bank over the distribution range of *A. saligna?*

2) What is the influence of abiotic and biotic factors on the seed bank dynamics?

3.2. Methods

3.2.1. Study site selection

Study sites were selected acording to the same procedures described in Chapter 2. The twenty five sites were selected to include as much environmental variation as possible (Figure 3.1 and Figure 3.2).

3.2.2. Study site description

Acacia saligna populations studied during this experiment were situated in the Western Cape with the exception of two Eastern Cape sites, Welgelegen and Kragga Kamma. Roughly two thirds of the Western Cape Port Jackson populations are situated along the west coast. Except for Travellers Rest, Romansrivier and Goudiniweg being situated on the eastern side of the north-south ranges of the Cape Fold Mountains, west coast sites are situated 12 – 45 km from the coast and between the coast and the western side of the Cape Fold Mountains paralleling the Atlantic Ocean. The remaining third of the *A. saligna* populations are situated 2 – 39 km from the coast and between

Figure 3.1: Satellite map indicating site positions across the distribution range of *A. saligna*. Travellers Rest – TR; Citrusdal – CD; Rietvlei – RV; Soutvlakte – SV; Veldrift – VD; Swartwater – SW; Yzerfontein –YF; Bossiesvlei – BV; Locheim – LH; Burgerspos – BP; Kanonkop –KK; Positano – PT; Romansrivier – RR; Goudiniweg – GW; Vergenoegd – VG; Hutch's Place – HP; Buffelsrivier – BR; Rooisand – RS; Coppul – CP; Modderrivier – RV; Fairfield – FF; Moreson – MS; Haasvlakte – HV; Welgelegen – WG; Kragga Kamma – KG. Yellow – West coast coastal; Pink – West coast inland; Dark blue – South coast coastal; Light blue – South coast inland; White – west coast eastern side of Cape Fold Mountains, Agterpakhuis; Green – west coast eastern side of Cape Fold Mountains, Bainskloof – Slanghoek; Red – Eastern Cape sites.

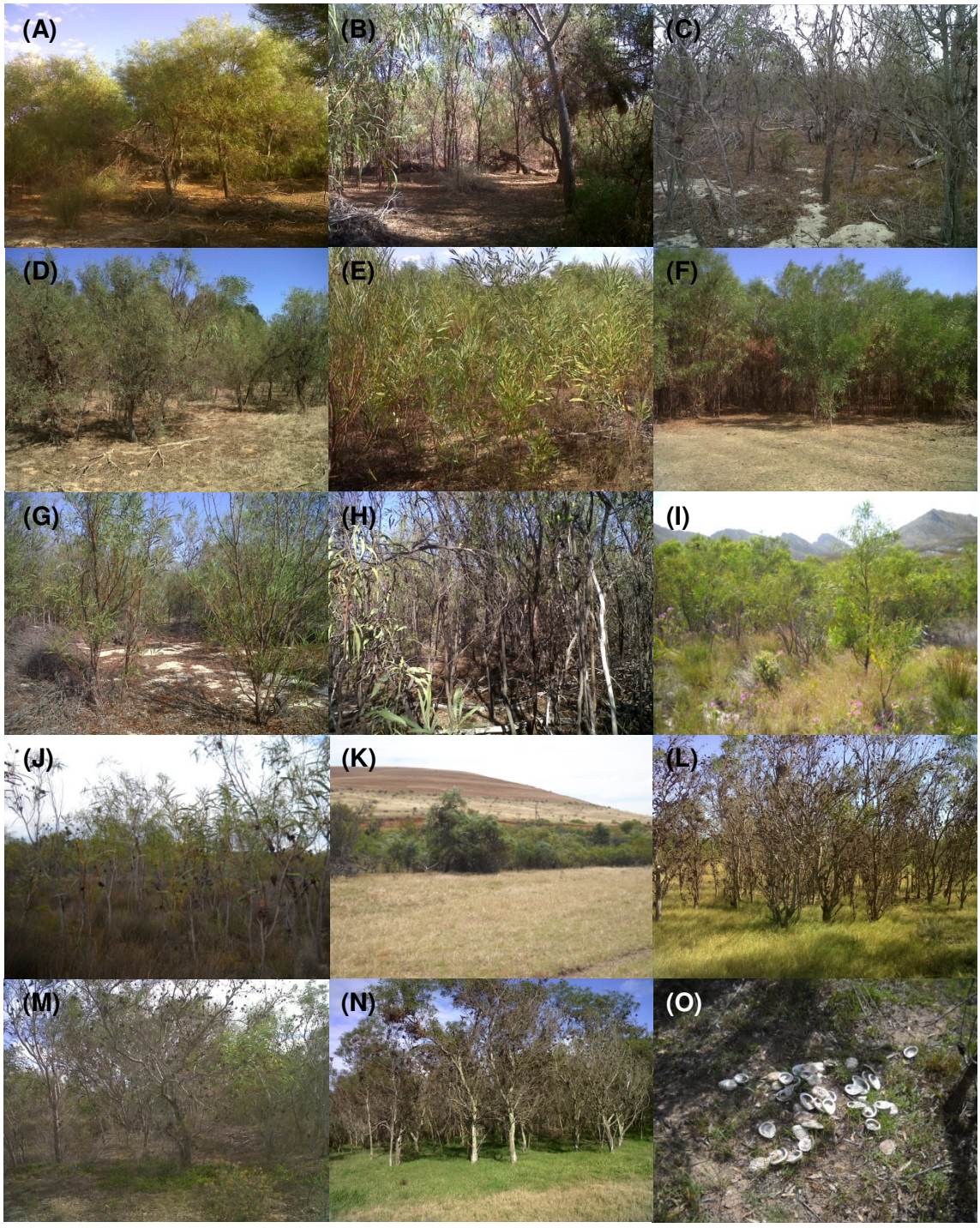

Figure 3.2: Photos showing the *A. saligna* populations of Travellers Rest (A), Citrusdal (B), Swartwater (C), Locheim (D), Romansrivier (E), Goudiniweg (F), Soutvlakte (G), Burgerspos (H), Buffelsrivier (I), Rooisand (J), Fairfield (K), Môreson (L), Haasvlakte (M) and Welgelegen (N). West coast coastal, (B); West coast inland, (D); South coast coastal, (I, J and M); South coast inland (K and L); Sites on eastern side of north-south range of Cape Fold Mountain (A, E and F), Eastern Cape site (N). Photo (O) is indicative of the shelter *A. saligna* populations provide for criminal activity (illegal perlemoen middens).

the coast and the west-east range of the Cape Fold Mountains. The sites can also be divided into coastal and inland sites. Coastal sites are within 25 km from the coast. Travellers Rest, Citrusdal, Rietvlei and Fairfield are situated along perennial watercourses. The two Eastern Cape sites are situated between Oesterbay and Port Elizabeth and are within 10 km from the coast.

3.2.3. Sampling procedures to estimate seed in the litter and soil – the seed bank

Data collection to estimate the number of seed in the litter layer and soil was conducted bi-annually, post and pre seed fall. December-March (summer) are the months during which seed are released from their pods and consequently fall to the ground and September-November (spring) are the months prior to seed fall (Holmes, 1990a; Holmes, 1990b). Sampling was done at the study sites during April 2010, November 2010 and April 2011.

Litter and soil samples were taken simultaneously, with the seed in the litter being removed first. A ring with a diameter of 10.5 cm was placed on the ground and the litter within the ring was collected. Afterwards a soil sample was taken at the same spot to a depth of 15 cm using a soil corer with a diameter of 5 cm and a length of 15 cm. Soil samples to a depth of 15 cm were taken as a previous study concluded that most seed are situated in the top 10 cm of the soil (Strydom *et al*., 2012). Fifty litter and soil samples were taken at each site during every sampling period. Fifty samples were taken as Strydom *et al*., (2012) determined that 30 – 50 samples are needed to accurately determine whether sites are different in terms of their seed bank. A random sampling technique was used to collect the litter and soil samples, as the seed bank of *A. saligna* in the top 10 cm of the soil has a clumped horizontal distribution (Strydom *et al*., 2012). The number of steps taken and the direction of movement between sampling points were determined from a random numbers table. Distance between samples was always 10 m or more. After the samples had been collected, the litter and soil samples were sieved through a 2 mm mesh and the number of seed in each sample was counted. The average number of seeds in the litter/soil/seed bank for every site and for every season, including the average over all three seasons was calculated. The combined data of all three seasons for the litter/soil/seed bank were subjected to an Anova test to determine whether sites were different in terms of these data. If sites were different in terms of their seed in the litter/soil/seed bank, these data were subjected to a multiple comparison of treatment by means test.

3.2.4. Abiotic and Biotic parameters

The summer aridity index (SAI), De Martonne aridity index (DMAI), winter concentration of precipitation (WCP), temperature of coldest month (TCM), soil texture, tree diameter, tree density and average number of galls per tree were estimated for the 25 study sites in the same manner as in Chapter 2. Tree diameter and tree density data were subjected to an Anova test to determine whether sites are different in terms of these measurements. If sites were different in terms of tree diameter or tree density, these data were subjected to a multiple comparison of treatment by means test. In addition, soil depth was also estimated for the seed bank experiments. To assess soil depth, a metal stake (1.5 cm thick) was hit as far as possible into the ground and the distance the stake moved into the soil was measured. This was repeated ten times at every site and the average soil depth was calculated. The measurement location was determined by the random sampling technique.

Seed viability at every site was determined. A hundred seed were taken at random from the seed collected in the soil from every site. Seed were chipped at the distal end and 25 seed were placed in each of 4 petri-dishes containing two filter paper discs filled with 10 ml water. Petri-dishes containing seed were placed in black plastic bags and incubated at 25 ˚C. After 3 days, seed were checked for germination and thereafter daily. Seed were evaluated to have germinated if the radicle was 1 mm long.

3.2.5. Climatic Indices

3.2.5.1 Winter concentration of precipitation (WCP)

The winter concentration of precipitation is a measure of the seasonality of rainfall (Bailey 1979). Winter concentration of precipitation is described by:

$$R = \frac{100\ (\text{sum of winter half precipitation})}{(\text{mean annual precipitation})}$$

with the sum of winter half precipitation being equal to the sum of the rainfall during April to September in mm.

3.2.5.2. De Martonne Aridity Index (DMAI):

De Martonne (1925) used the following equation to describe the aridity of a region:

$$H = \frac{P}{T+10}$$

where P is the annual precipitation in mm and T is the annual mean temperature in degrees centigrade. This index measures the precipitation effectiveness or aridity in a locality. Aridity is the extent to which a climate is deficient in life-promoting moisture (American Meteorological Society, 2011).

3.2.5.3. Summer aridity index (SAI)

The SAI is defined as "the sum of the mean precipitation for the four hottest months of the year, taken as a natural logarithm for scaling purposes and subtracted from a constant to ensure ascending values with increasing aridity" (Westfall and Rutherford, 1986). The index is summarized by:

$$SAI = 9 - \ln\left[\sum_{i=1}^{4} Pi\right]_{t_{max}}$$

where P is mean monthly precipitation in mm and the four hottest months in the study area are December–March. The index is an indication of the moisture content of the atmosphere during a period of the year that is physiological important including under conditions of high evaporation demand (Westfall and Rutherford, 1986).

3.2.3. Analysis

3.2.3.1. Statistical software and methods used

Data were analyzed with the statistical software R (R core development team, 2011) and the R package for Generalized linear mixed models (GLMMs), *lme4* (Bates *et al*., 2011). GLMMs were fitted to the seed in the litter, soil and seed bank data. GLMMs were used as the seed in the litter, soil and seed bank (response variables) were count data with Poisson distributions and only two

random effects were apparent in the study (Bolker *et al*., 2009). The GLMMs were fitted with a log link function and the Laplace approximation was used to estimate the parameters of the fitted models. The Laplace approximation rather than likelihood methods of estimation was employed as the number of seed per sample was occasionally less than 5 and only 2 random effects are present (Bolker *et al*., 2009). To obtain minimal adequate models, we removed stepwise backward all fixed effects as long as this caused no significant decrease in the model fit as assessed by the model AIC values (Crawley, 2005). After minimal adequate models were acquired, models were compared through the use of information theoretic (I-T) model procedures (McCarthy, 2007; Burnham *et al*., 2011). This was done to determine which model, within the model set, had the highest probability of being closest to "full reality" as well as to determine how much certainty there is around the prediction (McCarthy, 2007; Burnham *et al*., 2011). AICc values for each model were computed and the model with the smallest information loss or shortest distance from "full reality" was chosen as the best model and was used to obtain a ranking of the rest through determining the Δ AICc for each model (Burnham *et al*., 2011).

Burnham *et al*., (2011) described Δ values as follows:

- Δ values in the range of 2 - 7 have some support and should rarely be dismissed.
- Δ values between 9 and 11 have relatively little support, as these models lose too much information about full reality relative to some other models in the set.
- Δ values greater than 20 have essentially no empirical support.

After Δ values for each model were determined these values were used to compute the probability, AICcWt (Akaike weight), of each model. Using the AICcWt of each model a 95 % confidence model set (combined AICcWt $\geq$0.95) was chosen from the initial model set. The same procedures were repeated on the 95 % confidence set. This was done to see whether model probabilities would improve in the absence of models that have little or no weight. Afterwards, for each fixed effect the Akaike weights for models where they were present in the 95 % confidence set was summed to determine the evidence for their effect (McCarthy, 2007). Model averaging was also used as there may be information in the other models in the 95 % confidence set that is not captured by the best model (McCarthy, 2007; Burnham *et al*., 2011). Model averaging gives an indication of how valid the parameter estimates of the models are through providing parameter confidence intervals (Burnham *et al*., 2011). According to the best model in the 95 % model set, the evidence for the parameter effects and the results of model averaging, inferences were made about the data.

3.2.3.2. Maximal models

Maximal models were built with seed in the litter, seed in the soil and seed in the seed bank as response variables respectively. Two random effects were used in maximal models, season and site. Season was included as a random effect in the models as conditions between seasons within a site will fluctuate with time and the effect of season on sites will be different. Site was included as a random effect as the conditions across sites vary in time and space. Furthermore maximal models with season both as fixed and random effect, only as fixed effect and only as random effect was built to determine whether season only influence the variation of seed in the litter/soil/seed bank, only the numbers of seed in the litter/soil/seed bank or both. Fixed effects were first tested for significant co-variation before the maximal models were built. Only fixed effects that did not significantly co-vary and had Pearson correlation coefficients of less than 0.8 were used together in models. It was determined that the WCP and SAI fixed-effects co-vary (Appendix B, Table B4). According to the above-mentioned procedure the following maximal models were built:

1. Maximal model containing tree diameter, tree density, DMAI, SAI, TCM, sand fraction, soil depth and season as fixed effects and season and site as random effects.
2. Maximal model containing tree diameter, tree density, DMAI, WCP, TCM, sand fraction, soil depth and season as fixed effects and season and site as random effects.
3. Maximal model containing tree diameter, tree density, DMAI, SAI, TCM, sand fraction, soil depth and season as fixed effects and only site as random effect.
4. Maximal model containing tree diameter, tree density, DMAI, WCP, TCM, sand fraction, soil depth and season as fixed effects and only site as a random effect.
5. Maximal model containing tree diameter, tree density, DMAI, SAI, TCM, sand fraction and soil depth as fixed effects and season and site as random effects.
6. Maximal model containing tree diameter, tree density, DMAI, WCP, TCM, sand fraction and soil depth as fixed effects and season and site as random effects.

3.3. Results

3.3.1. Environmental Factors

3.3.1.1. Climatic factors

Altitude generally increases from the coast, inland (Table 3.1). When sites with similar distances from the coast are compared, sites along the south coast tend to be situated at lower altitudes than sites along the west coast. Along the west coast sites situated closer to the equator tend to be located at higher altitudes when sites of similar longitude are compared.

De Martonnes aridity index (DMAI) generally increases along the west coast from Clanwilliam towards Cape Town, moving from arid, to semi-arid, to Mediterranean to a semi-humid climate (Table 3.1). Along the south coast the DMAI generally decrease and then increase again from Cape Town towards Port Elizabeth, moving from semi-humid, to Mediterranean, to semi-arid and then again to Mediterranean and finally towards a semi-humid climate. The south coast sites in this study are generally characterised by higher DMAI when compared to the west coast sites. The coastal sites tend to have higher DMAI than inland sites of similar longitude or latitude along the coastal plain of the west coast or south coast respectively.

The summer aridity index (SAI) generally decreases from Clanwilliam towards Cape Town (west coast) (Table 3.1). From Cape Town towards Port Elizabeth there is a further decrease in the SAI (south coast). Therefore, Clanwilliam and Port Elizabeth represent the lowest and highest extremes respectively for the SAI. The coastal sites tend to have higher SAIs than inland sites of similar longitude or latitude along the coastal plain of the west and south coast respectively.

The winter concentration of precipitation (WCP) of the *A. saligna* populations along the west coast is generally higher than that of the *A. saligna* populations along the south coast (Table 3.1). West coast sites are characterised by winter rainfall regimes except for Burgerspos, Romansrivier and Goudiniweg which are characterised by strong winter rainfall regimes. Along the coastal plains parallel to the west-east ranges of the Cape Fold Mountains the WCP gradually decrease from Cape Town towards Port Elizabeth, moving from winter to even to summer rainfall regime. However, none of the sites in this study were characterised by a summer rainfall regime. When the moisture matrix of the SAI and the WCP of the *A. saligna* sites in the study are compared to the moisture matrix of the SAI and WCP in Rutherford and Westfall (1986) the sites were situated in the Fynbos biome except for Travellers Rest, Citrusdal, Rietvlei, Soutvlakte, Veldrift and Goudiniweg which are situated in the succulent Karoo biome.

Table 3.1:
Altitude (Alt), De Martonnes aridity index (DMAI), summer aridity index (SAI), mean annual precipitation (MAP), winter concentration of precipitation (WCP), mean annual temperature (MAT) and the temperature of the coldest month (TCM) for 25 *A. saligna* populations in South Africa.

Site	Co-ordinates	Coastal or Inland	Alt (m)	DMAI	SAI	MAP (mm)	WCP (%)	MAT (˚C)	TCM (˚C)	River or Stream	Grass cover	Biome
Travellers Rest	S 32° 04' E 19° 04'	Inland	314	7.9	5.58	235	78	20	7	River	No	SK
Citrusdal	S 32° 35' E 18° 60'	Inland	169	9.5	5.63	274	79	19	4	Stream	No	SK
Rietvlei	S 32° 38' E 18° 30'	Coastal	130	11.5	5.30	323	74	18	6	Stream	Yes	SK
Soutvlakte	S 32° 48' E 18° 22'	Coastal	58	13.4	5.57	378	78	18	6	No	No	SK
Veldrift	S 32° 51' E 18° 03'	Coastal	84	7.8	5.68	260	80	24	8	No	No	SK
Bossiesvlei	S 33° 12' E 18° 40'	Inland	158	14.7	5.18	422	79	19	8	Stream	No	FB
Locheim	S 33° 13' E 18° 40'	Inland	132	14.7	5.18	422	79	19	8	No	Yes	FB
Swartwater	S 33° 16' E 18° 15'	Coastal	91	16.3	5.31	456	78	18	8	No	No	FB
Yzerfontein	S 33° 20' E 18° 14'	Coastal	95	16.3	5.31	456	78	18	8	No	No	FB
Romansrivier	S 33° 28' E 19° 12'	Inland	269	22.1	4.75	615	79	18	7	No	No	FB
Burgerspost	S 33° 31' E 18° 32'	Coastal	114	23.9	5.19	668	83	18	8	No	No	FB
Kanonkop	S 33° 33' E 18° 33'	Coastal	265	17.0	5.06	452	79	17	6	No	No	FB
Goudiniweg	S 33° 38' E 19° 18'	Inland	235	20.5	5.69	570	81	18	4	No	No	SK
Positano	S 33° 39' E 18° 05'	Inland	123	25.1	4.75	711	81	18	8	No	No	FB
Vergenoegd	S 34° 02' E 18° 04'	Coastal	20	21.7	4.94	604	80	18	7	No	No	FB
Hutch's Place	S 34° 15' E 18° 26'	Coastal	93	13.1	5.04	357	74	17	11	No	Yes	FB
Buffelsrivier	S 34° 20' E 18° 51'	Coastal	66	19.6	4.90	545	72	18	9	No	No	FB
Rooisand	S 34° 20' E 19° 05'	Coastal	16	19.6	4.90	545	72	18	9	No	No	FB
Coppul	S 34° 25' E 19° 25'	Coastal	21	21.9	4.38	601	65	17	8	No	Yes	FB
Modderrivier	S 34° 26' E 19° 31'	Coastal	27	26.5	4.11	747	63	18	9	No	No	FB
Fairfield	S 34° 24' E 19° 48'	Inland	120	14.8	4.51	398	61	17	5	Stream	Yes	FB
Haasvlakte	S 34° 36' E 19° 52'	Coastal	42	20.1	4.54	546	66	17	9	No	No	FB
Môreson	S 34° 30' E 20° 01'	Inland	95	14.8	4.51	398	61	17	5	No	Yes	FB
Kragga Kamma	S 33° 56' E 25° 29'	Coastal	199	23.0	4.03	628	59	17	11	No	Yes	FB
Welgelegen	S 34° 10' E 24° 42'	Coastal	69	23.0	4.03	628	59	17	11	No	Yes	FB

Italics indicates sites that are situated along the south coast; Sites not in italics are those along the west coast; Bolded sites are situated in the Eastern Cape; Sites not in bold indicates those situated in the Western Cape; Underlined sites are situated on the eastern side of the north-south ranges of the Cape Fold Mountains; SK indicates Succulent Karoo biome; FB indicates Fynbos biome. De Martonne aridity index may be classified as follows: Arid, H<10; Semi-Arid, 10≤H≤20; Mediterranean, 20≤H≤24; Semi-Humid, 24≤H≤28; Humid, 28≤H≤35; Very Humid, 35≤H≤55; Extremely Humid, H≤55 (Baltas, 2007); Bailey's (1979) classification of WCP: Strong Winter, ≥81%; Winter, 61-80%; Even, 41-60%; Summer, 21-40%; Strong Summer ≤20%.

The temperature of the coldest month generally increases along the west coast from Clanwilliam towards Cape Town. There is a further increase in the TCM along the south coast from Cape Town towards Port Elizabeth. Therefore, the SAI and TCM both form gradients along the west and south coast's (Table 3.1).

3.3.1.2. Edaphic factors

Sand formed the largest component of soil texture for all the sites studied (Table 3.2). Moving from the coast inland the sand fraction tends to decline. Silt generally forms the largest fraction of the soil texture after sand and tends to increase the most as the sand fraction decreases. The clay fraction was generally the smallest soil texture component with only one study site having a clay component larger than 7 %. Most of the soils of the study sites can be classified as sand, followed by loamy sand and finally sandy loam. Although sand was the largest component of all the soils, the study sites differed in their large, medium, fine and very fine sand composition (Appendix E, Table E1). No particular pattern is evident for the soil depth. Furthermore, sites differed in the number of rocks they have per m^{-2} (Personal observation). The sand fraction and soil depth was not correlated (Pearsons correlation coefficient = 0.2).

3.3.2. Biological Factors

The south coast *A. saligna* populations tend to have trees that are currently smaller in size than the west coast sites (Table 3.3). Most of the trees of the west coast sites are significantly larger in stem diameter than the trees of the south coast sites. As tree size is also a proxy for tree age (Wood and Morris, 2007) the south coast *A. saligna* populations are assumed to be younger. Tree diameter also tends to decline with tree density, although this relationship is not significant (Figure 3.3). Tree density tends to be high when tree diameter is small and after recent fires (Figure 3.3; Table 3.4). Sites that have never been burnt tend to have lower tree densities when compared to sites that have been burnt under similar climatic conditions. No clear pattern seems to be apparent when tree densities of the west coast sites are compared to that of the south coast sites.

Generally the average number of galls on *A. saligna* increases with an increase in the tree diameter (Figure 3.4). The rate of increase in the number of galls with tree diameter for *A. saligna* is higher in areas characterised by lower SAIs. Coastal sites with an SAI>5 tend to have higher gall rust infections when compared to inland sites with an SAI>5. This is also the case for riparian *A. saligna* populations, with an SAI>5, with Rietvlei (coastal) having higher gall rust infection than Travellers Rest (Inland) (Table 3.3). This pattern is not apparent for coastal and inland sites with an SAI<5.

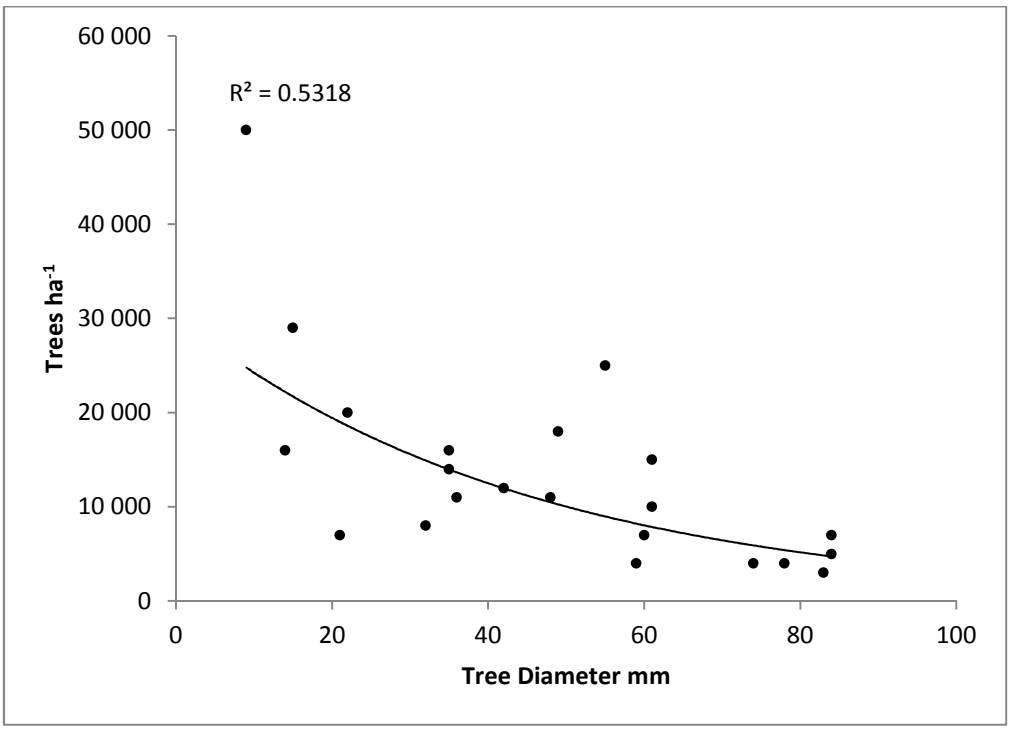

Figure 3.3: Indicates relationship between average tree size and density of the *A. saligna* study sites. (Pearsons correlation coefficient = -0.65).

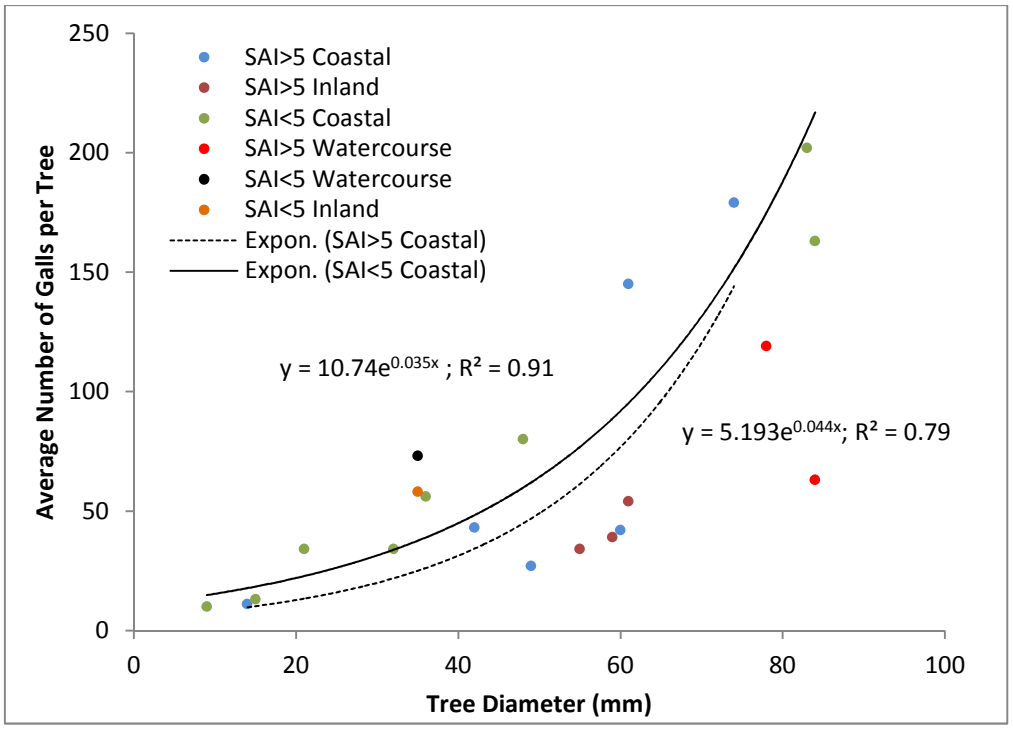

Figure 3.4: Indicates the relationship between tree diameter and the average number of galls per tree with sites divided into groups according to the summer aridity index (SAI). (Pearsons correlation coefficient = 0.77 for coastal SAI>5; Pearson = 0.98 for coastal SAI<5).

Table 3.2:
The sand, silt and clay fraction of each soil, consequent soil texture classification and soil penetrability of the *A. salgina* study sites.

SITE	Sand (%)	Silt (%)	Clay (%)	Soil classification	Soil Depth
Travellers Rest	86	10	4	Sand	62
Citrusdal	71	22	7	Sandy Loam	51
Rietvlei	98	0	2	Sand	43
Soutvlakte	94	5	1	Sand	67
Veldrift	93	8	0	Sand	88
Bossiesvlei	78	22	0	Loamy Sand	16
Locheim	65	30	5	Sandy Loam	14
Swartwater	93	6	1	Sand	48
Yzerfontein	95	0	4	Sand	22
Romansrivier	78	10	12	Sandy Loam	12
Burgerspost	93	5	2	Sand	23
Kanonkop	96	2	3	Sand	17
Goudiniweg	90	10	1	Sand	18
Positano	62	38	0	Sandy Loam	10
Vergenoegd	88	11	1	Sand	28
Hutch's Place	96	2	2	Sand	24
Buffelsrivier	90	5	5	Sand	10
Rooisand	91	8	1	Sand	25
Coppul	80	18	3	Loamy Sand	20
Modderrivier	96	4	0	Sand	12
Fairfield	88	9	3	Sand	5
Haasvlakte	90	10	1	Sand	7
Môreson	76	17	7	Loamy Sand	13
Kragga Kamma	83	11	6	Loamy Sand	17
Welgelegen	76	18	6	Loamy Sand	18

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Table 3.3:
Average tree diameter (±SD), tree density and galls per tree for 25 *A. saligna* sites.

Site	Tree Diameter (mm)	Similarity	Tree density mean (ha^{-1})	Similarity	Galls per tree	Seed viability (%)
Travellers Rest	84 ± 58	B,C	7 440 ± 7 682	E,F,G,H	63	98
Citrusdal	78 ± 42	A	3 600 ± 2 315	G,H,I	119	100
Rietvlei	41 ± 30	I,J	57 040 ± 47 824	A	150	99
Soutvlakte	42 ± 24	H,I	12 480 ± 6 678	C,D,E,F	43	90
Veldrift	74 ± 52	C,D	3 840 ± 1 315	G,H,I	179	96
Bossiesvlei	61 ± 41	D,E,F	14 880 ± 12 494	C,D,E	54	90
Locheim	59 ± 20	C,D,E	3 920 ± 2 105	G,H,I	39	92
Swartwater	60 ± 38	D,E,F	7 440 ± 5 174	E,F,G,H	42	100
Yzerfontein	61 ± 55	E,F,G	9 600 ± 7 526	D,E,F,G,H	145	96
Romansrivier	15 ± 9	N	29 120 ± 10 490	A,B	13	96
Burgerspost	49 ± 27	F,G	17 840 ± 7 635	B,C,D	27	99
Kanonkop	14 ± 4	N	16 400 ± 6 369	B,C,D	11	94
Goudiniweg	55 ± 28	G,H	24 560 ± 25 384	B,C	34	99
Positano	83 ± 40	A,B	2 560 ± 1 081	H,I	202	97
Vergenoegd	0 ± 0	P	0 ± 0	I	0	98
Hutch's Place	0 ± 0	P	0 ± 0	I	NA	94
Buffelsrivier	22 ± 14	M	19 760 ± 17 955	B,C,D	NA	92
Rooisand	32 ± 17	L	8 080 ± 3 166	D,E,F,G,H	34	92
Coppul	9 ± 4	O	50 000 ± 18 659	A	10	94
Modderrivier	21 ± 11	M	6 560 ± 4 114	E,F,G,H	34	100
Fairfield	35 ± 41	L	14 160 ± 5 189	B,C,D,E	73	97
Haasvlakte	48 ± 42	H,I	11 360 ± 8 336	C,D,E,F,G	80	99
Môreson	35 ± 19	J,K	16 080 ± 13 710	C,D,E	58	99
Kragga Kamma	36 ± 15	K,L	11 200 ± 5 177	C,D,E,F	56	100
Welgelegen	84 ± 35	A	4 640 ± 1 403	F,G,H	163	98

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Table 3.4:
Site history in terms of invasion history age and time since last fire (in years) for the 25 *A. saligna* study sites.

Site	Invasion History	Stand Age	Time since last fire
Travellers Rest	30+	10+	10
Citrusdal	26+	12+	12
Rietvlei	23+	3+	3
Soutvlakte	80+	4	NB
Veldrift	10+	10+	NA
Bossiesvlei	80+	10+	NA
Locheim	80+	15	12
Swartwater	23+	16+	12
Yzerfontein	NA	NA	NA
Romansrivier	NA	3+	3
Burgerspost	23+	18+	16
Kanonkop	NA	5+	NB
Goudiniweg	NA	NA	NA
Positano	NA	NA	NA
Vergenoegd	20+	2	2
Hutch's Place	20+	0	NA
Buffelsrivier	24+	2.5+	NB
Rooisand	NA	NA	MARCH 2011
Coppul	23+	NA	NA
Modderrivier	50+	5-6	NB
Fairfield	12+	12+	NA
Haasvlakte	64+	10	10
Môreson	10	10	NB
Kragga Kamma	NA	NA	NA
Welgelegen	23	23	NB

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3.3.3. Seed in the litter

The seed in the litter was generally large over all three sampling seasons with a range of 0 to 5 393 seed m^{-2} for sampling season 1 (post-dehiscence 2010), 0 to 4 278 seed m^{-2} for sampling season 2 (pre-dehiscence 2010) and 0 to 6 010 seed m^{-2} for sampling season 3 (post-dehiscence 2011) and 0 to 4 317 seed m^{-2} over all three seasons (Table 3.5). The seed in the litter layer is also characterised by larger levels of variation with the standard deviation being generally larger than the average estimated seed m^{-2} in the litter layer. When the seed m^{-2} in the litter layer in season 1 and season 2 are compared no general pattern of increase or decline is apparent. The seed in the litter layer m^{-2} for the third sampling season tends to be higher when compared to the other two sampling seasons. Sites with a grass cover, very dense stands and sites that experienced a recent fire usually have few seeds m^{-2} in the litter layer. Furthermore when sites of similar age and SAI are compared, also taking into account grass cover, tree density, time since last fire, invasion history and moisture regime (riparian, non-riparian, coastal or inland) a general pattern becomes apparent where the seed m^{-2} is higher in older stands characterised by moister conditions during the hot summer months conditions (See Appendix B, Table B1).

3.3.4. Seed in the soil

The seed in the soil m^{-2} was generally large over all three sampling seasons with a range of 224 to 31 923 seed m^{-2} for sampling season 1 (post-dehiscence 2010), 132 to 26 351 m^{-2} during sampling season 2 (pre-dehiscence 2010), 896 to 31 291 seed m^{-2} for sampling season 3 (post-dehiscence 2011) and 418 to 27 984 seed m^{-2} over all three sampling seasons (Table 3.6). The seed in the soil m^{-2} is characterised by large variation as is indicated by the standard deviation generally being high. Although the seed in the soil increased and decreased at sites from the first to the second sampling season no general pattern over all the sites was apparent. The seed in the soil m^{-2} was generally higher during the third sampling season when compared to the first and second sampling seasons. When sites with similar tree size and SAI are compared, taking into account invasion history and time since last fire event, a general pattern becomes apparent where the seed m^{-2} is higher in older stands characterised by moister conditions during the hot summer months (Appendix B, Table B2). The seed in the litter and soil are not correlated and therefore the number of seed in the litter is not indicative of the number of seed in the soil.

Table 3.5:
Average number (±SD) of seed in the litter per season as well as over all three sampling seasons (Season 1 – April 2010; Season 2 – November 2010; Season 3 – April 2011) for every study site.

Site	Season 1	Season 2	Season 3	Average over all seasons	Similarity
Travellers Rest	5 393 ± 6 842	1 139 ± 1932	4 804 ± 5 460	3 779 ± 5 477	C
Citrusdal	1 610 ± 2 033	2 665 ± 2 609	3 107 ± 9 678	2 461 ± 5 899	D,E
Rietvlei	543 ± 1 626	340 ± 767	1 296 ± 2 706	726 ± 1 908	I
Soutvlakte	1 494 ± 1 370	938 ± 878	2 873 ± 2 431	1 768 ± 1 865	C,D,E
Veldrift	1 194 ± 2 025	478 ± 885	3 141 ± 2 967	1 604 ± 2 403	F
Bossiesvlei	855 ± 1 067	670 ± 675	2 051 ± 3 838	1 192 ± 2 397	F
Locheim	441 ± 1 163	208 ± 452	245 ± 249	298 ± 737	I
Swartwater	850 ± 1 233	2 388 ± 2 584	3 719 ± 3 234	2 319 ± 2 742	C,D
Yzerfontein	557 ± 554	700 ± 770	621 ± 903	626 ± 753	H
Romansrivier	125 ± 283	141 ± 632	1 633 ± 7 205	633 ± 4 211	J
Burgerspost	393 ± 504	845 ± 1021	1 557 ± 967	932 ± 982	F,G
Kanonkop	5 ± 23	2 ± 16	0 ± 0	2 ± 16	L
Goudiniweg	1 647 ± 1 619	4 278 ± 2864	5 326 ± 4 874	3 750 ± 3 712	B
Positano	1 425 ± 1 410	1 506 ± 1 776	1 869 ± 2 067	1 600 ± 1 770	E
Vergenoegd	0 ± 0	0 ± 0	0 ± 0	0 ± 0	L
Hutch's Place	NA	NA	NA	NA	NA
Buffelsrivier	9 ± 39	5 ± 23	143 ± 366	52 ± 221	K,L
Rooisand	196 ± 404	457 ± 550	0 ± 0	218 ± 434	J
Coppul	7 ± 49	2 ± 16	0 ± 0	3 ± 30	L
Modderrivier	462 ± 597	935 ± 1 062	1 409 ± 1 132	935 ± 1 030	F
Fairfield	293 ± 415	626 ± 762	1 511 ± 1296	810 ± 1 032	G,H
Haasvlakte	2 899 ± 2 318	4 042 ± 3 343	6 010 ± 4 079	4 317 ± 3 546	A
Môreson	1 725 ± 2670	2 381 ± 3852	3 314 ± 2519	2 474 ± 3 121	C,D,E
Kragga Kamma	0 ± 0	111 ± 231	268 ± 791	126 ± 485	K
Welgelegen	NA	NA	NA	NA	NA

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Table 3.6:
Average number (±SD) of seed in the soil per season as well as over all three sampling seasons (Season 1 – April 2010; Season 2 – November 2010; Season 3 – April 2011) for every study site.

Site	Season 1	Season 2	Season 3	Average over all seasons	Similarity
Travellers Rest	31 923 ± 26 117	7 344 ± 10 165	21 686 ± 21 263	20 318 ± 22 567	D
Citrusdal	11 255 ± 10 037	26 331 ± 23 027	20 647 ± 20 381	19 411 ± 19 570	D
Rietvlei	5 164 ± 9 819	1 915 ± 4 252	5 511 ± 8 505	4 197 ± 8 005	J
Soutvlakte	11 154 ± 9 397	5 521 ± 6 820	8 108 ± 6 655	8 261 ± 8 015	E
Veldrift	9 931 ± 11 199	4 248 ± 7 544	8 597 ± 13 144	7 592 ± 11 077	F,G
Bossiesvlei	26 310 ± 24 642	26 351 ± 13 841	31 291 ± 17 381	27 984 ± 19 172	A
Locheim	12 855 ± 8 937	19 180 ± 10 249	24 375 ± 17 790	18 803 ± 13 683	B,C
Swartwater	19 221 ± 18 892	16 980 ± 13 060	17 367 ± 20 875	17 856 ± 17 825	C,D
Yzerfontein	2 485 ± 5 327	3 942 ± 3823	6 774 ± 13 866	4 400 ± 8 976	H,I
Romansrivier	2 485 ± 3 675	3 259 ± 4 757	4 553 ± 12 274	3 433 ± 7 884	H,I,J
Burgerspost	21 197 ± 12 775	21 696 ± 15 391	20 148 ± 10 879	21 014 ± 13 073	B
Kanonkop	2 170 ± 2 247	1 497 ± 1 726	1 803 ± 1 548	1 823 ± 1 872	J
Goudiniweg	6 285 ± 6 778	3 820 ± 3 674	8 801 ± 8 213	6 302 ± 6 775	F,G
Positano	19 150 ± 11 998	15 360 ± 13 263	22 063 ± 12 695	18 858 ± 12 875	B
Vergenoegd	1 334 ± 2 091	1 019 ± 1 758	968 ± 2 640	1 107 ± 2 185	K
Hutch's Place	3 881 ± 4 081	5 113 ± 5 650	6 570 ± 6 120	5 188 ± 5 432	G
Buffelsrivier	224 ± 516	132 ± 338	896 ± 1 532	418 ± 1 007	L
Rooisand	2 913 ± 4 012	4 461 ± 4 025	2 394 ± 2 703	3 256 ± 3 715	H
Coppul	1 406 ± 2 608	886 ± 1 349	2 200 ± 3 053	1 497 ± 2 489	K
Modderrivier	448 ± 695	1 029 ± 2 186	1 406 ± 1 648	961 ± 1 667	K
Fairfield	1 752 ± 2 734	2 302 ± 3 193	4 431 ± 6 483	2 828 ± 4 580	I,J
Haasvlakte	6 906 ± 9 193	6 081 ± 7 968	8 495 ± 9 048	7 160 ± 8 753	F
Môreson	4 482 ± 4 352	4421 ± 6 279	6 020 ± 5 320	4 974 ± 5 390	G
Kragga Kamma	7 161 ± 4 050	6 641 ± 4 150	7 925 ± 4 255	7 242 ± 4 158	E
Welgelegen	3 799 ± 2 666	5 928 ± 5 073	6 264 ± 7 044	5 331 ± 5 322	F,G

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Table 3.7:
Average number of seed in the seed bank per season as well as over all three sampling seasons (Season 1 – April 2010; Season 2 – November 2010; Season 3 – April 2011) for every study site.

Site	Season 1	Season 2	Season 3	Average over all seasons	Similarity
Travellers Rest	37 316 ± 27 655	8 483 ± 10 585	26 490 ± 23 676	24 096 ± 24 801	B,C,D,E
Citrusdal	12 865 ± 10 742	28 996 ± 23 426	23 753 ± 24 542	21 872 ± 21 492	C,D,E,F
Rietvlei	5 707 ± 10 288	2 254 ± 4 501	6 806 ± 10 100	4 923 ± 8 877	L
Soutvlakte	12 648 ± 9 742	6 459 ± 6 885	10 981 ± 7 703	10 029 ± 8 555	F,G
Veldrift	11 125 ± 11 493	4 726 ± 7 560	11 738 ± 13 720	9 196 ± 11 793	H,I
Bossiesvlei	27 165 ± 25 139	27 021 ± 14 038	33 342 ± 19 898	29 176 ± 20 288	A
Locheim	13 296 ± 8 869	19 388 ± 10 394	24 620 ± 17 829	19 101 ± 13 693	A,B,C
Swartwater	20 071 ± 18 917	19 368 ± 13 396	21 086 ± 20 921	20 175 ± 17 920	A,B,C,D
Yzerfontein	3 042 ± 5 310	4 642 ± 3 923	7 395 ± 13 725	5 026 ± 9 068	J,K
Romansrivier	2 610 ± 3 681	3 400 ± 4 772	6 186 ± 18 898	4 066 ± 11 478	L
Burgerspost	21 590 ± 12 807	22 541 ± 15 222	21 705 ± 11 104	21 945 ± 13 072	A,B
Kanonkop	2 174 ± 2 243	1 500 ± 1726	1 803 ± 1 548	1 826 ± 1 870	L
Goudiniweg	7 932 ± 7 070	8 097 ± 5 336	14 127 ± 9 914	10 052 ± 8 154	E,F,G
Positano	20 575 ± 12 304	16 866 ± 13 409	23 931 ± 13 239	20 457 ± 13 226	A,B,C
Vergenoegd	1 334 ± 2 091	1 019 ± 1 758	968 ± 2 640	1 107 ± 2 185	O
Hutch's Place	3 881 ± 4 081	5 113 ± 5 650	6 570 ± 6120	5 188 ± 5 432	I,J
Buffelsrivier	233 ± 530	137 ± 337	1 040 ± 1 556	470 ± 1 045	P
Rooisand	3 109 ± 4 038	4 919 ± 4 186	2 394 ± 2 703	3 474 ± 3 830	K
Coppul	1 413 ± 2 606	888 ± 1 347	2 200 ± 3 053	1 500 ± 2 488	N
Modderrivier	910 ± 1 036	1 964 ± 2 376	2 815 ± 2 070	1 896 ± 2 057	K,L
Fairfield	2 045 ± 2 872	2 928 ± 3 384	5 941 ± 6 789	3 638 ± 4 944	K
Haasvlakte	9 805 ± 9 929	10 123 ± 9182	14 505 ± 11 224	11 478 ± 10 306	D,E,F
Môreson	6 207 ± 5 820	6 802 ± 7 150	9 334 ± 5819	7 448 ± 6 398	G,H
Kragga Kamma	7 161 ± 4050	6 752 ± 4 163	8 193 ± 4 192	7 368 ± 4 152	F,G
Welgelegen	3 799 ± 2 666	5 928 ± 5073	6 264 ± 7 044	5 331 ± 3 238	H,I

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3.3.5. Seed bank size

The seed bank m^{-2} was generally large over all three sampling seasons with a range of 233 to 37 316 seed m^{-2} for sampling season 1 (post-dehiscence 2010), 137 to 28 996 m^{-2} during sampling season 2 (pre-dehiscence 2010), 968 to 33 342 seed m^{-2} for sampling season 3 (post-dehiscence 2011) and 470 to 29 176 seed m^{-2} over all three sampling seasons (Table 3.7). The seed bank m^{-2} is characterised by large variation as is indicated by the standard deviation generally being high. However, the variation in the seed bank is lower than the variation of the seed in the litter layer and in the soil. The seed bank size both increased and decreased at sites from the first to the second sampling season and no general pattern over all the sites was apparent. The seed bank m^{-2} was generally higher during the third sampling season when compared to the first and second sampling seasons. When sites with similar tree size and SAI are compared, taking into account invasion history, time since last fire event and moisture regime (riparian, non-riparian, coastal or inland) a general pattern becomes apparent where the seed m^{-2} in the seed bank is higher in older stands characterised by moister conditions during the hot summer months (Appendix B, Table B3).

3.3.6. Glmer results

3.3.6.1. Seed in the leaf-litter

The estimates of tree diameter, SAI, TCM and the sand fraction were significant (all p-values <0.05) in the best model when the seed in the litter was used as the response variable (Table 3.8). The seed in the litter increased with tree diameter and the sand fraction and decreased with the SAI and TCM. The best model fitted the data well (Appendix B, Figure B1). The evidence for the effects of tree diameter, SAI and TCM on the number of seed in the litter is very strong as the sum of the Akaike weights for the models in which they are present is 1 (Table 3.9 and Table 3.10). The sum of the Akaike weights for the models in which the SAI and WCP is present is weak, 0.51 and 0.49 respectively. This is the result of SAI being absent in the models where the WCP is present. The sum of the Akaike weights for SAI and WCP combined is equal to 1. Therefore there is strong evidence for the effect of the SAI and WCP on the number of seed in the litter. The relationship of seed in the litter with tree diameter, SAI, TCM, sand fraction and WCP was also determined as valid through model averaging procedures as their confidence interval did not include 0 (Table 3.11). The evidence for the effects of the other explanatory variables in the leaf litter 95 % confidence set models (Table 3.9) is low (AICcWt < 0.4) and there is doubt around their validity as their confidence limit intervals included 0 (Table 3.9). Therefore, there is strong evidence for the

Table 3.8:
Results of best model with seed in the leaflitter as response variable, with data analysed with a Generalized linear mixed model fit by the Laplace approximation for a Poisson distribution.

Fixed effect	Estimate ± SE	z-value	p-value
Intercept	2.56 ± 4.44	0.58	0.565
Tree Diameter	0.33 ± 0.06	5.80	$6.81e^{-9}$
SAI	-1.94 ±0.93	-2.07	0.038
TCM	-0.43 ± 0.19	-2.22	0.027
Sand Fraction	0.08 ± 0.03	2.19	0.029

Model AIC value: 46 210;Model deviance: 46 188 Random effects: Site, StDev = 1.31; Season 2, StDev = 0.89; Season 3, StDev = 1.75; Sitefactor: 23

Table 3.9:
Combined Akaike weights (AICcWt) for every fixed effect in the models where they were present in the litter, soil and seedbank models.

Site	Litter	Soil	Seedbank
Tree diameter	1.00	0.99	1.00
SAI	0.51	0.59	0.41
TCM	1.00	0.23	0.00
Sand fraction	1.00	0.09	0.00
DMAI	0.69	0.73	0.46
WCP	0.49	0.20	0.11
Season 2	0.34	0.99	1.00
Season 3	0.34	0.99	1.00
Tree Density	0.14	0.23	0.07
Soil Depth	0.03	0.83	0.43

Table 3.10:
95% Model set with seed in the litter as response variable- Model selection based on AICc.

MODEL	K	AICc	∆AICc	AICcWt	Cum.Wt	LL
Model 1	11	46210.41	0.00	0.21	0.21	-23094.17
Model 2	12	46210.42	0.02	0.21	0.41	-23093.17
Model 3	14	46211.45	1.04	0.12	0.54	-23091.66
Model 4	13	46211.83	1.43	0.10	0.64	-23092.86
Model 5	12	46212.03	1.63	0.09	0.73	-23093.97
Model 6	13	46212.29	1.88	0.08	0.81	-23093.09
Model 7	15	46213.34	2.93	0.05	0.86	-23091.60
Model 8	14	46213.36	2.96	0.05	0.91	-23092.62
Model 9	13	46213.65	3.24	0.04	0.95	-23093.77
Model 10	14	46214.22	3.82	0.03	0.98	-23093.05
Model 11	15	46214.94	4.53	0.02	1.00	-23092.40

Table 3.11:
Multi model inference on predictors (fixed effects) in models in confidence set (Best models for the litter models).

Fixed effect	Estimate ± SE	Confidence limit interval
Tree Diameter	0.35 ± 0.06	0.24 to 0.46
SAI	-1.99 ± 0.96	-3.86 to -0.11
TCM	-0.44 ± 0.19	-0.81 to -0.06
Sand Fraction	0.08 ± 0.03	0.01 to 0.14
DMAI	0.13 ± 0.09	-0.04 to 0.30
WCP	-0.11 ± 0.04	-0.20 to -0.03
SEASON 2	0.18 ± 0.20	-0.20 to 0.56
SEASON 3	0.62 ± 0.33	-0.03 to 1.27
Soil Depth	-0.01 ± 0.02	-0.05 to 0.03
Tree Density	0.11 ± 0.23	-0.35 to 0.57

Table 3.12:
Results of best model with seed in the soil as response variable, with data analysed with a Generalized linear mixed model fit by the Laplace approximation for a Poisson distribution.

Fixed effect	Estimate ± SE	z-value	p-value
Intercept	0.84 ± 1.28	0.66	0.509
Tree Diameter	0.09 ± 0.01	5.93	$3.07e^{-9}$
DMAI	-0.06 ±0.03	-2.14	0.032
WCP	0.02 ± 0.02	1.61	0.108
Soil penetrability	-0.02 ± 0.01	-2.54	0.011
Season 2	-0.09 ± 0.11	-0.86	0.392
Season 3	0.29 ± 0.09	3.23	0.001

Model AIC value: 48 446; Model deviance: 48 420; Random effects: Site, StDev = 0.9; Season 2, StDev = 0.54; Season 3, StDev = 0.44; Sitefactor: 25

Table 3.13:
95% Model set with seed in the soil as response variable- Model selection based on AICc.

MODEL	K	AICc	∆AICc	AICcWt	Cum.Wt	LL
Model 1	13	48446.03	0.00	0.13	0.13	-24209.96
Model 2	12	48446.40	0.37	0.11	0.24	-24211.16
Model 3	12	48446.47	0.44	0.10	0.34	-24211.19
Model 4	13	48446.58	0.55	0.10	0.44	-24210.24
Model 5	16	48446.65	0.63	0.09	0.53	-24207.25
Model 6	15	48446.67	0.65	0.09	0.63	-24208.27
Model 7	10	48446.68	0.65	0.09	0.72	-24213.31
Model 8	11	48447.15	1.12	0.07	0.79	-24212.54
Model 9	14	48447.19	1.16	0.07	0.87	-24209.54
Model 10	14	48447.30	1.28	0.07	0.93	-24209.60
Model 11	15	48447.40	1.37	0.07	1.00	-24208.63

Table 3.14:
Multi model inference on predictors (fixed effects) in models in confidence set (Best models for the soil models).

Fixed effect	Estimate ± SE	Confidence limit interval
Tree Diameter	0.085 ± 0.017	0.052 to 0.199
DMAI	-0.058 ± 0.031	-0.120 to 0.003
WCP	0.027 ± 0.016	-0.004 to 0.058
Soil Depth	-0.019 ± 0.008	-0.035 to -0.003
SEASON 2	-0.094 ± 0.110	-0.310 to 0.121
SEASON 3	0.292 ± 0.091	0.115 to 0.470
SAI	0.638 ± 0.371	-0.089 to 1.365
Tree Density	0.120 ± 0.087	-0.050 to 0.290
Sand Fraction	-0.023 ± 0.014	-0.050 to 0.003
TCM	0.112 ± 0.072	-0.028 to 0.253

Table 3.15:
Results of best model with seed in the seedbank as response variable, with data analysed with a Generalized linear mixed model fit by the Laplace approximation for a Poisson distribution.

Fixed effect	Estimate ± SE	z-value	p-value
Intercept	7.36 ± 0.28	26.3	$<2e^{-16}$
Tree Diameter	0.09 ± 0.02	5.69	$1.26e^{-8}$
Season 2	-0.06 ±0.11	-0.57	0.57
Season 3	0.36 ± 0.09	3.86	0.0001

AIC value:24647077;Model deviance: 24647057 Random effects: Site, StDev = 0.86; Season 2, StDev = 0.53; Season 3, StDev = 0.46; Sitefactor: 25

Table 3.16:
95% Model set with seed in the seedbank as response variable - Model selection based on AICc.

MODEL	K	AICc	ΔAICc	AICcWt	Cum.Wt	LL
Model 1	10	24647077	0.00	0.23	0.23	-12323529
Model 2	11	24647078	0.41	0.19	0.42	-12323528
Model 3	11	24647078	0.82	0.15	0.57	-12323528
Model 4	12	24647079	1.39	0.12	0.69	-12323527
Model 5	12	24647079	1.68	0.10	0.79	-12323527
Model 6	13	24647079	2.29	0.07	0.86	-12323527
Model 7	13	24647080	2.40	0.07	0.93	-12323527
Model 8	14	24647081	3.59	0.04	0.97	-12323526
Model 9	14	24647081	3.94	0.03	1.00	-12323527

Table 3.17:
Multi model inference on predictors (fixed effects) in models in confidence set (Best models for the seedbank models).

Fixed effect	Estimate ± SE	Confidence limit interval
Tree Diameter	0.088 ± 0.017	0.055 to 0.121
SEASON 2	-0.061 ± 0.107	-0.271 to 0.149
SEASON 3	0.359 ± 0.094	0.175 to 0.543
SAI	0.425 ± 0.313	-0.189 to 1.040
DMAI	-0.041 ± 0.032	-0.104 to 0.022
Soil Depth	-0.011 ± 0.009	-0.028 to 0.005
WCP	0.021 ± 0.017	-0.012 to 0.054
Tree Density	0.082 ± 0.093	-0.099 to 0.264

effect of tree size and age, water availability during summer, minimum temperature and soil texture on the number of seed in the litter-layer along the south and west coast in South Africa. The GLMMs results support the observations for seed in the litter layer m^{-2} as it indicates that for the majority of sites, which receive their water through rainfall, less seed will be produced with an increase in the SAI and when sites of similar SAI are compared the coastal sites will have more seed m^{-2} than the inland sites as indicated by more seed being present in sites with a greater sand fraction. Consequently, the results of the GLMMs with seed in the litter as response variable support the previous observations made of the seed in the litter layer being larger m^{-2} in locations experiencing more moist conditions during the hot summer months. However, sites along watercourses, when grass cover is taken into account, are exceptions generally having more seed in the litter layer m^{-2}. The seed in the litter m^{-2} will therefore increase from Clanwilliam towards Cape Town and further from Cape Town towards Port Elizabeth for non-riparian *A. saligna* populations. The seed in the litter m^{-2} for riparian *A. saligna* populations will increase from Port-Elizabeth towards Cape Town and from Cape Town towards Clanwilliam. However, this pattern for riparian and non-riparian *A. saligna* populations can only be described with certainty for the Western Cape sites as both Eastern Cape sites had a grass cover, but an absent or mainly absent litter layer.

3.3.6.2. Seed in the soil

The estimates of tree diameter, DMAI, soil depth and the third sampling season were significant (all p-values <0.05) in the best model when seed in the soil was used as the response variable (Table 3.12). The seed in the soil increased with tree diameter and the third sampling season and decreased with the DMAI and soil depth. The best model fitted the data well (Appendix B Figure 2B). The evidence for the effects of tree diameter and sampling season on the seed in the soil is very strong as the sum of the Akaike weights for the models where they are present is 1 (Table 3.9 and Table 3.13). The combined sum of the Akaike weights for the models were DMAI, soil penetrability and the other explanatory variables are present is low and therefore there is little evidence that they affect the seed in the soil. The relationship of seed in the soil with tree diameter and the third sampling season was the only explanatory variables determined as valid through model averaging procedures as their confidence interval did not include 0 (Table 3.14). Therefore, there is strong evidence for the effect of tree size and age and sampling season and consequently also the passage of time on the seed in the soil. The GLMMs support the observation that older sites produce more seed. The seed in the soil follows the same pattern across its distribution as the seed in the litter layer once *A. saligna* populations with similar average size trees, invasion history and SAI are compared (Appendix B, Table B2).

3.3.6.3. The seed bank

The estimates of tree diameter and third sampling season were significant (all p-values <0.05) in the best model when seed in the seed bank was used as the response variable (Table 3.15). The seed in the seed bank increased with tree diameter and the third sampling season. The model is not a very good fit for the data (Appendix, Figure 3B). However, this is probably because the data for the seed in the litter and soil had to be transformed to seed m^{-2} to allow for the addition of these two parameters as their sampling units differed, leading to the deviance of data points from the value predicted by the best model being many times greater. The evidence for the effect of tree diameter and sampling season on the seed bank is very strong as the sum of the Akaike weights for the models where they are present is 1 (Table 3.9 and Table 3.16). The relationship of seed in the seed bank with tree diameter and the third sampling season was the only explanatory variables determined as valid through model averaging procedures as their confidence interval did not include 0 (Table 3.17). Therefore, there is strong evidence for the effect of tree size and age and sampling season and consequently also the passage of time on the seed bank. The GLMMs results are similar to the results with seed in the soil as response variable. This is not surprising as the seed in the soil comprise the largest constituent of the seed bank.

3.4. Discussion

The seed bank was assessed to be large over the sampled distribution of *A. saligna* in South Africa 470 to 29 176 seed m^{-2}. The seed bank of *A. saligna* was characterised by large variations in seed abundance m^{-2} within sites and over its distribution. The size of the *A. saligna* trees, the availability of moisture during the hot summer months and coarser texture soil was assessed to be important factors governing the seed bank dynamics of *A. saligna.*

3.4.1. Seed in the leaf litter

Large seed numbers in the leaf litter of *A. saligna* stands were generally present at all sites during all three sampling seasons with the exception of sites that recently burned, experienced cyclic mechanical clearing and/or had grass cover. However, no clear pattern of increase or decline in litter seed abundance between sampling seasons was evident. The lack in pattern may be ascribed to the large variation of seed abundance in the litter layer spatially. Romansrivier illustrates this best, having a standard deviation 4 times the size of the average seed in the litter m^{-2}. The variation of seed numbers in the litter layer in space and time is likely a consequence of many factors including seed production (Richardson and Kluge, 2008), abiotic dispersal

processes (Tozer, 1998), ant burial (Holmes, 1990a; Holmes, 1990b; Tozer, 1998; French and Major, 2001; Richardson and Kluge, 2008), predation (Milton and Hall, 1981; Holmes, 1990a; Holmes, 1990b; Richardson and Kluge, 2008), rotting (Milton and Hall, 1981; Holmes, 1989; Holmes, 1990b), fire events (Richardson and Kluge, 2008), passive movement into the soil and germination (Milton and Hall, 1981). Furthermore the topography of the landscape (Gutiérrez *et al*., 2000; Caballero *et al*., 2003; Caballero *et al*., 2005) and vegetation structure (Caballero *et al*., 2003; Caballero *et al*., 2005, Caballero *et al*., 2008b) of *A. saligna* populations will be important in determining where seed accumulate.

Over its distribution range *A. saligna* had more seed m^{-2} in the litter layer as population tree size and age increased. Larger Port Jackson trees will produce more seed as they have more resources to allocate to reproduction and will have more new shoots to initiate flower formation (Goal and Fox, 2002). *Acacia saligna* populations also tend to increase the available nutrients in the soil over time which will lead to older stands having higher growth rates and reproduction (Yelenik *et al*., 2004). Processes negatively affecting seed residence time in the litter might also decrease with *A. saligna* stand age such as passive and active dispersal of seed. Older *A. saligna* populations will accumulate more leaf litter underneath their canopy, which may restrict horizontal seed movement. Areas with longer invasion histories will transform the environment to a greater degree, decreasing native diversity (French and Major, 2001, Holmes, 2002) and leading to decreased seed predation and ant burial (Holmes, 1990a; Holmes, 1990b).

Fewer seed m^{-2} reside in the leaf litter in areas receiving less rainfall during the summer months as indicated by the relationship of seed m^{-2} in the litter with the summer aridty index (SAI) and winterconcentration of precipitation (WCP). This is similar to the findings of Chapter 2 which found that *A. saligna* populations produce more seed in environments experiencing moister summer conditions. Other studies in semi-arid environments have also shown that more seed are produced during years which receive more rainfall (Gutiérrez *et al*., 2000; Caballero *et al*., 2008). This is not only the case for water limited environments as water was assessed as important for seed production under other climatic regimes (Matlack *et al*., 1990; Bossuyt and Hermy, 2001; Stark *et al*., 2008). Higher reproduction of *A. saligna* populations in moister conditions during summer months may be ascribed to more resources within a season and over time being available for maintenance, growth and reproduction (Goal and Fox, 2002). Consequently, there should be a general increase in the seed in the litter of sites of similar age along the west coast from Clanwilliam towards Cape Town and from Cape Town towards Port Elizabeth. This is at least generally the case for the seed in the leaf litter in the Western Cape as the Eastern Cape sites had a grass cover present. However there are also exceptions to this pattern in the Western Cape. The exceptions include *A. saligna* populations with grass cover and stands situated along watercourses. In the case of populations with grass cover, less seed were present. This may be the consequence of less leaf litter accumulating in these stands with seed being incorporated

faster into the soil as seed fall through the grass leaves directly to the soil surface. It may also be that predation and decay is higher under these circumstances. Larger quantities of seed m^{-2} are present in the litter layer in *A. saligna* populations situated along watercourses e.g. rivers. *Acacia saligna* populations along watercourses will produce more seed m^{-2} as they will have a faster growth rate and more resources to allocate to reproduction (Milton 1980; Chapter 2).

Soil texture influenced the presence of seed in the litter layer, with coarser textured soil having more seed m^{-2}. The greater numbers of seed m^{-2} in the litter is probably a result of the effect soil texture has on water availability. Finer textured soils have slower water infiltration rates and loose more water to evapotranspiration than coarser textured soils (Fravolini *et al*., 2005). Therefore, during the summer months more water will be available in the coarse textured soil leading to greater seed production. Sand fractions of the soil of *A. saligna* populations were larger closer to the coast. Consequently, coastal *A. saligna* populations should have more seed m^{-2} in the litter layer than inland populations of similar age and climatic conditions. This result was also apparent in Chapter 2. The exceptions to this pattern are *A. saligna* populations with grass cover and populations along watercourses.

Acacia saligna populations in areas characterised by warmer winter temperatures (within the range of 4 – 11 ˚C) had less seed m^{-2} in the leaf-litter. This might indicate that *A. saligna* populations require winter conditions that are well defined from summer months by colder temperatures to initiate flowering. Therefore according to temperature of the coldest month (TCM) the seed m^{-2} in the leaf-litter should generally decrease along the west coast from Clanwilliam towards Cape Town (north to south) and further along the south coast from Cape Town towards Port Elizabeth (West to East). However, the TCM might reflect the influence of grass cover on the seed in the litter layer as most of the sites with a grass cover was situated along the south coast and *A. saligna* populations with grass covers tend to have little or no seed in the leaflitter. Therefore the decline in seed m^{-2} with the increase in the TCM might rather reflect the incluence of the grass cover on seed production.

3.4.2. Seed in the soil

Soil seed abundance was high during all three sampling seasons. Seed viability was high (90 - 100 %) at all the study sites, similar to findings in other studies (Holmes *et al*., 1987, Holmes, 1988, Jefferey *et al*., 1988). The soil seed reserves m^{-2} of the *A. saligna* populations were characterised by large spatial variation as was found by other seed bank studies (Esler and Boucher, 2004, Caballero *et al*., 2005). The variation of the seed in the soil may primarily be attributed to germination (Milton and Hall, 1981; Holmes, 1988; Holmes, 1989; Esler and Boucher, 2004; Richardson and Kluge, 2008), decay (Milton and Hall, 1981; Holmes, 1989; Richardson and

Kluge, 2008), pathogenic attack (Holmes, 1989), fire (Morris, 1997; Morris, 1999; Holmes, 2002; Richardson and Kluge, 2008) and further dispersal down the soil profile (Milton and Hall, 1981; Esler and Boucher, 2004). Smaller soil seed reserves were usually the result of a more recent disturbance event (Holmes *et al*., 1987; Morris, 1997; Esler and Boucher, 2004), e.g. fire which will lead to either seed destruction or germination.

The seed in the soil shows a definite increases during the third sampling season (post-dehiscence April 2011) which was absent during the second sampling season (pre-dehiscence November 2010). Therefore the seed in the soil will largely increase during the months *A. saligna* releases its seed (December-March). This may be because the probability of seeds finding a place where it will be rapidly incorporated into the soil (e.g. soil crack, loose sandy soil etc.) being larger during primary dispersal. This will be as the number of seed that is dispersed at one time is the largest during this period, increasing the chance of seeds finding a suitable location for incorporation into the soil. Once seed are on the soil surface they may remain stationary for long periods of time in the "unsuitable" location (e.g. rock surface, thick litter layer etc.) before secondary dispersal processes result in their incorporation into the soil. Less seed will also be dispersed simultaneously during secondary dispersal from "unsuitable sites" decreasing the chance of seed being incorporated into the soil. Exceptions to the increase of the seed in the soil during the third sampling season may be the result of lower reproduction as a consequence of seasonal variation in the climate with time.

The seed in the soil showed no clear pattern of increase or decline between the first (April 2010 post-dehiscence) and second sampling season (November 2010, pre-dehiscence). This may be attributed to seed being continually added from the litter layer to the soil seed reserve as a consequence of secondary dispersal and processes leading to seed decline varying in time and space. However, factors influencing seed decline in the soil is smaller than the annual input resulting in the accumulation of large *A. saligna* soil seed reserves. Although the addition of seed to the soil differs in space and time, all *A. saligna* populations eventually accumulate large soil seed reserves over its distribution range in South Africa.

The soil seed reserve is greater under the canopy of *A. saligna* populations with larger trees. Larger *A. saligna* trees will have a greater capacity for reproduction (Goal and Fox, 2002) and will have had more opportunities to reproduce and accumulate seed in the soil as they are assumed to be older. This is consistent with the increase in the size of the seed bank during the third sampling season as more seed will accumulate over time in the soil (Holmes, 1989).

The reason for the soil seed reserve not showing an association with other abiotic and biotic factors can be attributed to its inherent ability to absorb adverse effects in space and time (Harper 1977; Louda, 1989, Caballero *et al*., 2005; Caballero *et al*., 2008b). However, the effects of abiotic and biotic factors on the soil seed reserve are more apparent when stands of similar age, invasion

history and disturbance frequency are compared. When stands of similar age are compared a similar pattern to that of the seed in the litter is apparent for the soil seed reserve. Seed in the soil reserve tends to be larger in areas with more moist summer conditions. Deviance from this pattern may be ascribed to different invasion histories and disturbance frequency. The effect of abiotic and biotic parameters on seed production is more evident in the litter as the residence time of seed in this layer is shorter and the ability to absorb seasonal and spatial effects is less.

When the above mentioned is taken into account the seed in the soil of *A. saligna* populations of similar age in non-riparian habitats should generally increase along the west coast from Clanwilliam toward Cape Town and further towards Port Elizabeth along the south coast, being larger closer to the coast. When sites along watercourses are considered, the accumulation of seed in the soil should be the largest in sites where winter temperatures becomes limiting later during the year. This pattern seems to be supported along the west coast and along the south coast at least as far as Bredasdorp. In the Eastern Cape the seed in the soil of Kragga Kamma supports this pattern but the seed in the soil of Welgelegen deviates from this pattern.

3.4.3. The combined seed bank

The results for the combined seedbank (i.e. litter and soil seed estimates combined) are the same as for the soil seed reserve. This is not surprising as the seed in the soil is many times larger than the seed in the litter, depending on age and last disturbance event e.g. the soil stored reserve is 23 times larger than the seed in the litter at Bossiesvlei. Therefore, the same conclusion can be made for the combined seed bank as for the seed in the soil, with *A. saligna* populations with larger trees producing more seed and having more seed m^{-2} under its canopy. When the seed bank is compared between sites of similar age, invasion history, and time since last disturbance, sites in more moist conditions tend to accumulate more seed. However, sites along watercourses are again the exception having more seed than sites only receiving precipitation through rainfall. The seed bank will therefore follow the same pattern as the seed in the soil along the west and south coast.

Milton (1980) postulated two situations limiting growth, run-off and run-on situations. She described growth being limited alternately by soil moisture and temperature. The same can be argued for seed production and consequent accumulation of seed in the seed bank as an indirect effect of water availability on growth. Therefore, *A. saligna* growing along river courses, around lakes and dams will not only have longer growing seasons and grow more rapidly but will also produce more seed and accumulate more seed in the seed bank as a consequence of it.

3.4.4. Tree Density

Tree density may follow two patterns: never burnt and burnt. First generation *A. saligna* stands, i.e. stands that have never been burnt, tend to have lower tree densities when compared to *A. saligna* populations of similar tree diameter which have been burnt. This is as the expansion of first generation sites are dependent on the "small" portion of seed that do germinate without fire treatment. Previous studies have determined that 2 % of *A. saligna* seed germinate without prior heat treatment (Milton, 1980). The densities of first generation stands will therefore increase slowly (lag phase), rapidly increase (exponential phase) and stabilise when the *A. saligna* population reach the carrying capacity of the area. The density of the stand will then fluctuate around this "equilibrium point" until the *A. saligna* population experience a large disturbance event.

In contrast, when a first generation *A. saligna* population is burnt and the whole above ground population is killed, there will be a rapid decrease in the tree density followed by a major increase in the tree density as the dormant seeds in the seed bank will germinate to a level above the carrying capacity of the area (Milton, 1980). The tree density will then decline towards the "equilibrium" tree density (Milton, 1980) which is a consequence of the available space and abiotic and biotic conditions of the area. In these circumstances, of the second generation, the age of the trees should be more similar over the invaded space. The similarity in tree age will be dependent on the ability of the fire to eliminate the trees of the previous generation. Therefore, it will be possible to have two stands with the same average tree diameter but with different tree densities.

Second generation *A. saligna* populations should accumulate seed banks faster than first generation stands with second generation populations of similar age and under similar abiotic conditions having larger seed banks m^{-2}. Second generation stands will accumulate larger seed banks as more trees ha^{-1} will be present over time in an area when compared to first generation stands covering a similar area and existing for a similar time period. All the *A. saligna* trees of second generation stands will also start producing seed at the same time. Therefore second generation populations will accumulate seed banks faster for a given time period when compared to a first genereation stand as they will have more trees and more constant seed input over the invaded area.

3.4.5. Gall Rust Fungus

The average number of galls per tree increased exponentially with an increase in tree diameter which is similar to findings of other studies (Morris, 1997). The rate of increase in the average number of galls per *A. saligna* tree is greater in areas with a lower SAI. The higher number of galls on *A. saligna* trees in more moist environments may be attributed to the trees having higher growth

rates under these conditions with more new growth available for infection. Furthermore moist conditions are also important for gall rust infection (Chapter 2). The direct effect of the galls, making *A. saligna* more susceptible to drought, should be greater along the west coast while the indirect effect, the infection of new expanding leaflets, shoots and reproductive structures should be the largest along the south coast. Therefore, in more water stressed areas the gall rust fungus will lead to more rapid tree mortality by making it more susceptible to drought, while in the more moist areas the fungus will have a larger effect on the newly formed reproductive structures as growth will be higher in these areas. Therefore more active management will be required in *A. saligna* populations that are situated in more moist conditions.

3.4.6. Management implications

3.4.6.1. Non-riparian *A. saligna* populations

When non-riparian *A. saligna* stands of similar age are compared the difficulty of eliminating their seed bank m^{-2} of in terms of rate of accumulation will generally increase from Clanwilliam towards Cape Town and further from Cape Town towards Port Elizabeth, with the coastal sites posing the largest threat. The difficulty to eliminate the seed bank m^{-2} of *A. saligna* will increase with the current age of the stand as well as time since first introduction into the area. The gall rust fungus should help management efforts the most along the west coast for non-riparian *A. saligna* populations. However, active management will be required to eradicate *A. saligna* populations.

3.4.6.2. Riparian *A. saligna* populations

When Riparian *A. saligna* stands of similar age are compared the difficulty of eliminating their seed bank m^{-2} in terms of rate of accumulation will generally decrease from Clanwilliam towards Cape Town and further from Cape Town towards Port Elizabeth, with the coastal sites posing the largest threat. The difficulty to eliminate the seed bank m^{-2} of *A. saligna* will increase with the current age of the stand as well as time since first introduction into the area. The gall rust fungus should help management efforts the most along the south coast for riparian *A. saligna* populations. This will be as the conditions favouring infection will be better along the south coast. However, active management will be required to eradicate *A. saligna* populations. Riparian *A. saligna* populations should generally pose a larger threat in terms of the seed bank than non-riparian *A. saligna* populations.

3.5. Conclusion

The seed production and seed bank of *A. saligna* is still large over its distribution range in South Africa. The availability of water during the hot summer months is the primary factor limiting seed bank size. Therefore climate and edaphic conditions are crucial in predicting the rate at which *A. saligna* will accumulate a persistent seed bank. After abiotic conditions, invasion history, time since last fire and population age are important in predicting seed bank size. The effect of the gall rust fungus is the most pronounced in more arid environments. Furthermore, *A. saligna* may rather die from old age in more moist conditions. Consequently *A. saligna* seed banks will be the largest in populations situated in riparian habitats, with a long invasion history, characterised by large trees and which has experienced a fire event during previous years. In conclusion, *A. saligna* populations still pose a large threat and constant active management is required to control and eradicate this invasive Australian *Acacia,* especially in conditions where water is readily available during the hot summer months.

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General Conclusion

In this thesis I explored the seed bank dynamics of *Acacia saligna*, an Australian *Acacia*, across its distribution in South Africa where it has become invasive. Specifically, I explored how the seed bank dynamics of *A. saligna* varies across time and space with different abiotic and biotic factors. An understanding of seed bank dynamics is of particular interest to managers, as this is one of the main components preventing the successful and sustainable removal of Port Jackson in South Africa, as for other invasive Australian *Acacias.* This is the first study to assess the seed bank dynamics of an invasive *Acacia* over such a large distribution and environmental gradient. This chapter presents overall conclusions of the work conducted for this study.

Chapter 2 investigated the seed production status of *A. saligna* across its distribution range in South Africa and determined the influence of different environmental factors on the variance of seed output in space and time. Water availability during the hot summer months was determined as the most important factor influencing the size of reproductive output, with seed production being larger with increasing moisture availability. *Acacia saligna* populations are classified as riparian and non-riparian, with these situations having important implications for the moisture availability during summer months which is a physiologically challenging time for plants. In non-riparian areas growth and reproduction is limited by both water and temperature, while in riparian areas growth and reproduction is limited only by temperature. The size of the trees is the next important factor influencing reproductive output. However, the influence of tree size and age on seed production only becomes apparent when the moisture regime is controlled for, with more seed being produced by larger trees.

In non-riparian situations the seed production will generally increase along the west coast from Clanwilliam towards Cape Town and further from Cape Town towards Bredasdorp, being larger closer to the coast. In riparian situations the seed production will generally increase along the south coast from Bredasdorp towards Cape Town and from Cape Town towards Clanwilliam, being larger closer to the coast. *Acacia saligna* populations generally produce more seed in riparian situations when compared to non-riparian situations. Although the rate at which the size of seed production increases with time in certain areas may be lower, the size of its reproductive output over its entire sampled distribution range is large.

In Chapter 3, the size of the seed in the litter layer, soil and consequent total seed bank was determined across *A. saligna's* distribution range in South Africa, examining how different environmental factors influence the variation of the seed in the litter layer, soil and seed bank in space and time. It was determined that time since invasion, size of the trees and current age of stand, time since last disturbance event and moisture availability during the summer months are important for determining which stands will have the largest seed bank as well as how fast seed

banks will accumulate. The findings of Chapter 3 are similar to that of Chapter 2 except when considering the number of seed in the soil, invasion history and time since last disturbance event becomes crucial for understanding the processes governing reproductive output.

The seed bank increases from Clanwilliam towards Cape Town and from Cape Town towards Port Elizabeth in non-riparian *A. saligna* populations. In riparian *A. saligna* populations the seed bank increases from Port Elizabeth towards Cape Town and further from Cape Town towards Clanwilliam. However, *A. saligna* seed banks tend to be larger in riparian situations than in non-riparian situations. Therefore the water regime of an area is crucial in determining how fast the seed bank will accumulate over time.

Therefore it can be concluded that the size of trees and the water regime is crucial for the size of the reproductive effort and the seed bank. The size of the trees over time will be a consequence of their growth rate. Therefore, in South Africa growth rate of *A. saligna* is possibly the primary factor limiting the size of reproduction spatially with water availability, temperature and the gall rust fungus being its primary constraints. Reproductive output is indirectly influenced by other abiotic and biotic factors through their effect on water availability and gall rust fungus infection and consequently on growth rate. Although the seed feeding weevil (*Melanterius compactus*) reduces the number of seed that will successfully establish in the future, the organism does not reduce the maximum potential output of the tree. Its success is rather determined by its ability to consume the seed output once it has been realized.

Early reproductive maturity is an inherent characteristic of *A. saligna* trees as a consequence of its fast growth rate. Therefore early reproductive maturity as a consequence of fast growth rate may be instrumental for the invasive success of *A. saligna* over its distribution in South Africa (Gibson *et al*., 2011). The rate of growth will also influence the rate at which *A. saligna* can transform its environment to make its characteristics more favourable for its own growth, reproduction and consequent survival.

Areas for further research

It will be of importance to evaluate the seed bank dynamics of other Australian *Acacia (*Wilson et al., 2011*),* including bird dispersed species*,* to determine whether this pattern is unique to *A. saligna* or whether this is a general pattern. This will be crucial as this will determine whether management can prioritise clearing programmes in a similar manner as for *A. saligna*.

Future studies need to assess the growth rate of Australian *Acacia* under different water regimes as this will give an indication of the time that is available to clear these trees before huge amount of resources will have to be spent.

More detailed studies are required to effectively understand the extent to which the gall rust fungus restricts growth under different water regimes and to formally quantify its indirect and direct effects (Wilson *et al*., 2011). This will be required in able to assess its effectiveness as a biological control agent and to separate its effect from other abiotic and biotic factors.

It will also be important to determine how many seed m^{-2} in the soil will translate into established seedlings m^{-2}. This will be a more accurate estimate of how large the threat of the seed bank will be in the future. Furthermore the number of seed required m^{-2} to successfully re-establish a population in the future needs to be estimated. This will be important as this will indicate with how much seed banks will have to be decreased to lead to population establishment failure.

It will also be valuable to determine the rate at which the density of *A. saligna* seedlings decreases over time under different water regimes. This will give management an idea of how long they must wait in order to spend the least amount of resources to clear *Acacia saligna* populations.

Studies determining how fast the seed bank of different Australian *Acacia* accumulates over time will also be important (Wilson *et al*., 2011).

The data of the study will also be very valuable in modelling invasion success and control as most models to date do not include detailed data of the seed bank dynamics (Gibson *et al*., 2011).

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Appendix A

GLMMs Statistical Analysis

Reason for exclusion from Chapter 2

The results for the seed pod rain and seed rain data fitted with GLMMs are shown below. The GLMMs result was not used as the data set is too small for the full model to be used. Furthermore the sites Travellers Rest, Rietvlei, Fairfield and Welgelegen are also sites that are exceptions as the first three are sites situated along watercourses and the last site is the site situated in the Eastern Cape. Travellers Rest, Fairfield and Rietvlei have large reproductive output in arid environment because of the presence of water throughout the year were as sites that are not situated along river courses, which is the norm, have smaller reproductive output as water becomes limiting during the hot summer months. Furthermore, the Eastern Cape, which has the lowest seed production estimates, is the site which sits at the one end of the environmental gradient, being the site with the lowest WCP and SAI, second lowest sand fraction and largest TCM all the sites. Welgelegen is also the site with the largest trees, lowest tree density and highest gall rust fungus estimate. Travellers Rest, the site with the largest seed production estimates, is at the other extreme end, being the sites with the highest SAI and lowest TCM. Travellers Rest also has a high WCP and sand fraction. Therefore, the small data set and the influence of sites parameters that could not be included in the GLMMs model exert an influence on the data that is larger than that of which the data of the other sites can correct for. Even if the model compensates for these differences in the random effects these influences are too great for the small data set. The description of how the analysis was done and how the models were build are described below after which the results are shown.

Statistical software and methods used

The data was analyzed with the statistical software R (R core development team, 2011) and the R package for GLMMs, lme4 (Bates *et al*, 2011). Generalized linear mixed models (GLMMs) were fitted to the seed pod rain and seed rain data. GLMMs were used as the seed pod rain and seed rain (response variables) were count data with Poisson distributions and only 2 random effects were apparent in the study (Bolker *et al*., 2009). The GLMMs were fitted with a log link function and the Laplace approximation was used to estimate the parameters of the fitted models. The Laplace approximation rather than likelihood methods of estimation was employed as the number of seed per trap was occasionally less than 5 and only 2 random effects are present (Bolker *et al*., 2009).

The full model, containing all the biotic and abiotic parameters as fixed effects, could not be used as there were insufficient degrees of freedom. The degrees of freedom allowed a maximum of 5 parameters to be used as fixed effects simultaneously in a single model. Furthermore, parameters were tested for covariance and only parameters that did not co-vary were used together in models. Therefore, models expected to best answer the research question were built manually.

After the parameters for every model were estimated, models were compared through the use of information theoretic (I-T) model selection procedures. This was done to determine which model, within the model set, had the highest probability of being closest to "full reality" as well as to determine how much certainty there is around the prediction. AICc values for each model were computed and the model with the smallest information loss or shortest distance from "full reality" was chosen as the best model and was used to obtain a ranking of the rest through determining the Δ AICc for each model (Burnham *et al*., 2011).

Burnham *et al*., (2011) described Δ values as follows:

- Δ values in the range of 2-7 have some support and should rarely be dismissed.
- Δ values between 9 and 11 have relatively little support, as these models lose too much information about full reality relative to some other models in the set.
- Δ values greater the 20 have essentially no empirical support).

After the Δ values for each model were determined these values were used to compute the AICcWt, of every model. Using the AICcWt of each model a 95% confidence model set was chosen from the initial model set. The same procedures were repeated on the 95% confidence set. This was done to see whether the probability of the models would improve in the absence of the models that are very far from "full reality". Afterwards model averaging was also used as there may be information in the other models in the 95 % confidence set not captured by the best model. Model averaging also gives an indication of how valid the parameter estimates of the models are through providing parameter confidence intervals (Burnham *et al*., 2011). According to the best model in the 95% model set and the results of model averaging inferences were made about the data.

Models in model set

Models were built with seed pod rain and seed rain as response variables respectively. Two random effects were apparent, the individual trees around which traps were placed and site. Individual trees were included as a random effect in the models as the number of seed produced per tree could vary between trees solely as consequence of the trees inherent characteristics. Site was added as a random effect as the conditions across sites vary in time and space. The following

fixed effects were used in the models: tree diameter, tree density, weevil damage, DMAI, SAI, WCP, TCM and sand fraction. Before the models were built the fixed effect were tested for covariance. It was determined that SAI and WCP co-varies. Therefore these two fixed effects were not used together in models. Models only included 5 fixed effects at most and were built as follows:

Models containing each fixed effect separately, to determine the influence of every individual parameter on the seed pod rain/seed rain.

Models containing combinations of only abiotic fixed effects

Models containing combinations of only biotic fixed effects

Every biotic model with an added one or two abiotic fixed effects.

This was done as the abiotic factors will exert pressure on the biotic factors which will translate into an effect expressed in the seed rain/seed pod rain. In the end 62 models out of all possible models were built.

Results for Seed pod GLMMs

Table A1:
Results of Best Model with Seed pod capsule rain as response variable, with data analysed with a Generalized linear mixed model fit by the Laplace approximation for a poisson distribution

Fixed effect	Estimate ± SE	z-value	p-value
Intercept	-4.14 ± 1.53	-2.7	0.007
DMAI	-0.08 ±0.03	-3	0.003
SAI	0.67 ± 0.23	2.9	0.004
TCM	-0.02 ± 0.78	-0.16	0.877
Sand Fraction	0.06 ± 0.01	6.45	$1.09e^{-10}$

Model AIC value: 2072;Model deviance: 2058 Random effects: Site, StDev = 0.12; Individual trees; StDev = 0.46; Sitefactor: 9

TABLE A2:
Multi model inference on predictors (fixed effects) in models in confidence set (Best models for the seed pod rain models)

Fixed effect	Estimate ± SE	Confidence limit interval
Weevil Damage	-0.001 ± 0.01	-0.03 to 0.02
DMAI	-0.10 ± 0.04	-0.18 to -0.03
SAI	0.68 ± 0.26	0.18 to 1.18
TCM	0.02 ± 0.11	-0.19 to 0.23
SAND	0.07 ± 0.01	0.05 to 0.09
WCP	0.03 ± 0.01	0.01 to 0.05
Tree Density	-0.03 ± 0.07	-0.17 to 0.10
Tree circumference	-0.03 ± 0.03	-0.09 to 0.03

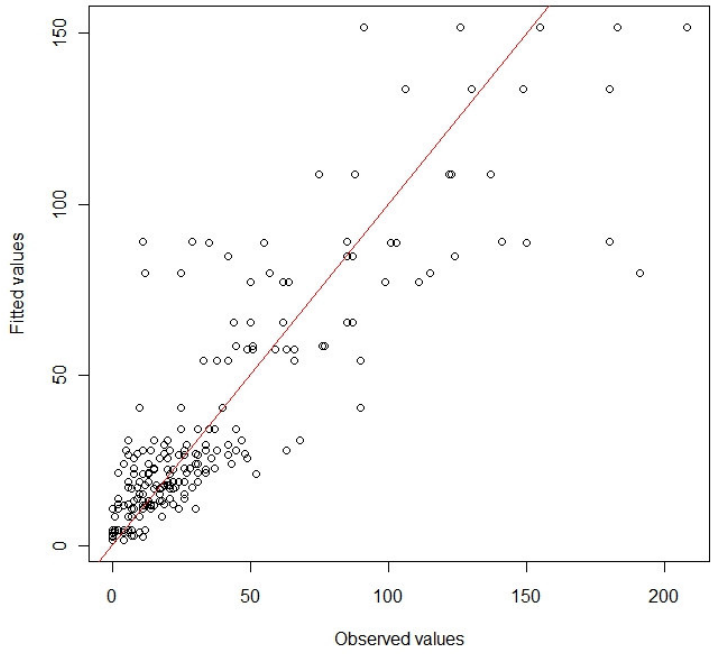

Figure 2.3: Indicates how well the glmer model fits the seed pod rain data.

Results for seed rain GLMMs

Table A3:
Results of Best Model with Seed rain as response variable, with data analysed with a Generalized linear mixed model fit by the Laplace approximation for a poisson distribution

Fixed effect	Estimate ± SE	z-value	p-value
Intercept	-4.14 ± 1.53	-2.84	0.004
Weevil Damage	-0.02 ± 0.1	-1.65	0.100
DMAI	-0.10 ±0.05	-2.00	0.046
SAI	0.92 ± 0.35	2.63	0.009
TCM	0.03 ± 0.09	-0.33	0.739
Sand Fraction	0.07 ± 0.01	7.82	$5.19e^{-15}$

Model AIC value: 1351;Model deviance: 1335 Random effects: Site, StDev = 0.00; Individual trees; StDev = 0.49; Sitefactor: 9

Table A4:
Multi model inference on predictors (fixed effects) in models in confidence set (Best models for the seed rain models)

Fixed effect	Estimate ± SE	Confidence limit interval
Weevil Damage	-0.02 ± 0.01	-0.05 to 0.01
DMAI	-0.12 ±0.05	-0.23 to 0.02
SAI	0.92 ± 0.35	0.23 to 1.61
TCM	-0.04 ± 0.09	-0.14 to 0.22
SAND	0.07 ± 0.01	0.05 to 0.09
WCP	0.04 ± 0.02	0.00 to 0.07

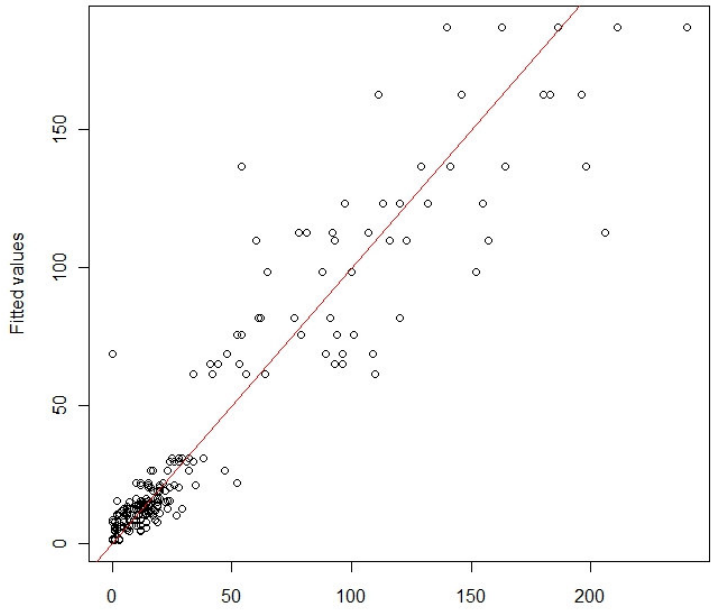

Figure 2.4: Indicates how well the glmer model fits the seed rain data.

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Appendix B

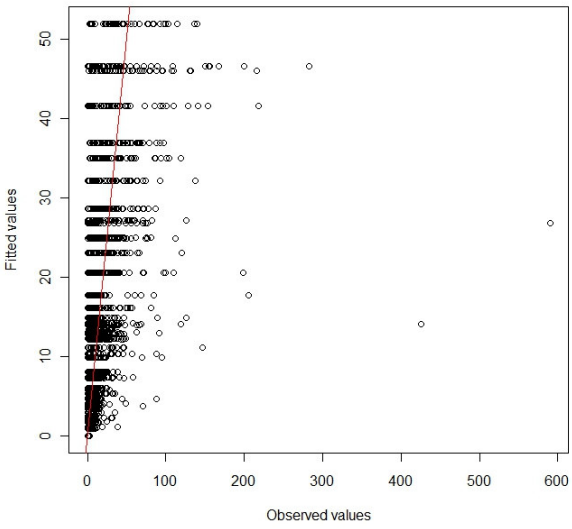

Figure B1: Indicates how well the glmer model fits the data for the seed in the litter.

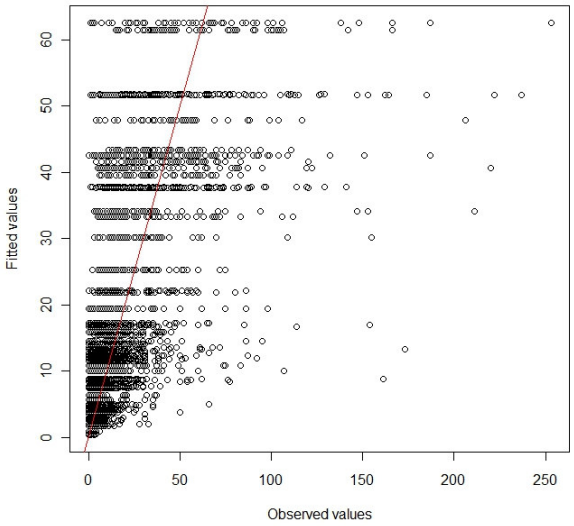

Figure B2: Indicates how well the glmer model fits the data of the seed in the soil.

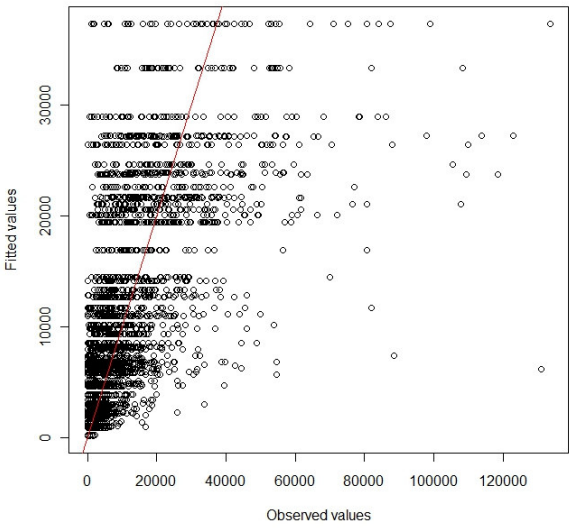

Figure B3: Indicates how well the glmer model fits the data for the seed in the seedbank.

Table B1:
The seed in the soil m^{-2} of sites that are similar in terms of their tree diameter are shown in similar columns (A-P) and sites are arranged according to their SAI.

Site	SAI	Tree Diameter	Grass Cover	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P
Goudiniweg	5.69	55 ± 28	No							3 750	3 750								
Veldrift	5.68	74 ± 52	No			1 604	1 604												
Citrusdal	5.63	78 ± 42	No	2 461															
Travellers Rest	5.58	84 ± 58	No		3 779	3 799													
Soutvlakte	5.57	42 ± 24	No								1 768	1 768							
Swartwater	5.31	60 ± 38	No				2 319	2 319	2 319										
Yzerfontein	5.31	61 ± 55	No					626	626	626									
Rietvlei	5.30	41 ± 30	Yes									726	726						
Burgerspost	5.19	49 ± 27	No						932	932									
Bossiesvlei	5.18	61 ± 41	No				1 192	1 192	1 192										
Locheim	5.18	59 ± 20	Yes			298	298	298											
Kanonkop	5.06	14 ± 4	No														2		
Hutch's Place	5.04	0 ± 0	Yes																NA
Vergenoegd	4.94	0 ± 0	No																0
Buffelsrivier	4.90	22 ± 14	No													418			
Rooisand	4.90	32 ± 17	No												218				
Romansrivier	4.75	15 ± 9	No														633		
Positano	4.75	83 ± 40	No	1 600	1 600														
Haasvlakte	4.54	48 ± 42	No								4 317	4 317							
Fairfield	4.51	35 ± 41	Yes												810				
Môreson	4.51	35 ± 19	Yes										2 474	2 474					
Coppul	4.38	9 ± 4	Yes															3	
Modderrivier	4.11	21 ± 11	No													961			
Kragga Kamma	4.03	36 ± 15	Yes											126	126				
Welgelegen	4.03	84 ± 35	Yes	NA															

Italics indicates sites that are situated along the south coast; Bolded sites indicates the Eastern Cape sites; Underlined sites are sites that are situated on the eastern side of the north-south ranges of the Cape Fold Mountains

Table B2:
The seed in the soil m^{-2} of sites that are similar in terms of their tree diameter are shown in similar columns (A-P) and sites are arranged according to their SAI.

Site	SAI	DMAI	Tree Diameter	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P
Goudiniweg	5.69	20.5	55 ± 28							6 302	6 302								
Veldrift	5.68	7.8	74 ± 52			7 592	7 592												
Citrusdal	5.63	9.5	78 ± 42	19 411															
Travellers Rest	5.58	7.9	84 ± 58		20 318	20 318													
Soutvlakte	5.57	13.4	42 ± 24								8 261	8 261							
Swartwater	5.31	16.3	60 ± 38				17 856	17 856	17 856										
Yzerfontein	5.31	16.3	61 ± 55					4 400	4 400	4 400									
Rietvlei	5.30	11.5	41 ± 30									4 197	4 197						
Burgerspost	5.19	23.9	49 ± 27						21 014	21 014									
Bossiesvlei	5.18	14.7	61 ± 41				27 984	27 984	27 984										
Locheim	5.18	14.7	59 ± 20			18 803	18 803	18 803											
Kanonkop	5.06	17	14 ± 4														1 823		
Hutch's Place	5.04	13.1	0 ± 0																5 188
Vergenoegd	4.94	21.7	0 ± 0																1107
Buffelsrivier	4.90	19.6	22 ± 14													418			
Rooisand	4.90	19.6	32 ± 17												3 256				
Romansrivier	4.75	22.1	15 ± 9														3 433		
Positano	4.75	25.1	83 ± 40	18 858	18 858														
Haasvlakte	4.54	20.1	48 ± 42								7 160	7 160							
Fairfield	4.51	14.8	35 ± 41												2 828				
Môreson	4.51	14.8	35 ± 19										4 974	4 974					
Coppul	4.38	21.9	9 ± 4															1 497	
Modderrivier	4.11	26.5	21 ± 11													961			
Kragga Kamma	4.03	23	36 ± 15											7 242	7 242				
Welgelegen	4.03	23	84 ± 35	5 331															

Italics indicates sites that are situated along the south coast; Bolded sites indicates the Eastern Cape sites; Underlined sites are sites that are situated on the eastern side of the north-south ranges of the Cape Fold Mountains

Table B3:
The seed in the soil m^{-2} of sites that are similar in terms of their tree diameter are shown in similar columns (A-P) and sites are arranged according to their SAI.

Site	SAI	DMAI	Tree Diameter	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P
Goudiniweg	5.69	20.5	55 ± 28							10 052	10 052								
Veldrift	5.68	7.8	74 ± 52			9 196	9 196												
Citrusdal	5.63	9.5	78 ± 42	21 872															
Travellers Rest	5.58	7.9	84 ± 58		24 096	24 096													
Soutvlakte	5.57	13.4	42 ± 24								10 029	10 029							
Swartwater	5.31	16.3	60 ± 38				20 175	20 175	20 175										
Yzerfontein	5.31	16.3	61 ± 55					5 026	5 026	5 026									
Rietvlei	5.30	11.5	41 ± 30									4 923	4 923						
Burgerspost	5.19	23.9	49 ± 27						21 945	21 945									
Bossiesvlei	5.18	14.7	61 ± 41				29 176	29 176	29 176										
Locheim	5.18	14.7	59 ± 20			19 101	19 101	19 101											
Kanonkop	5.06	17	14 ± 4														1 826		
Hutch's Place	5.04	13.1	0 ± 0																5 188
Vergenoegd	4.94	21.7	0 ± 0																1107
Buffelsrivier	4.90	19.6	22 ± 14													470			
Rooisand	4.90	19.6	32 ± 17												3 474				
Romansrivier	4.75	22.1	15 ± 9														4 066		
Positano	4.75	25.1	83 ± 40	20 457	20 457														
Haasvlakte	4.54	20.1	48 ± 42								11 478	11 478							
Fairfield	4.51	14.8	35 ± 41												3 638				
Môreson	4.51	14.8	35 ± 19										7 448	7 448					
Coppul	4.38	21.9	9 ± 4															1 500	
Modderrivier	4.11	26.5	21 ± 11													1 896			
Kragga Kamma	4.03	23	36 ± 15											7 368	7 368				
Welgelegen	4.03	23	84 ± 35	5 331															

Italics indicates sites that are situated along the south coast; Bolded sites indicates the Eastern Cape sites; Underlined sites are sites that are situated on the eastern side of the north-south ranges of the Cape Fold Mountains

Table B4
Indicates the correlation coefficients of the different fixed effects

	Tree Diameter	Tree Density	Soil penetrability	Sand Fraction	WCP	TCM	DMAI	SAI
Tree Diameter	1.000							
Tree Density	-0.376	1.000						
Soil penetrability	0.445	-0.126	1.000					
Sand Fraction	-0.310	0.188	0.264	1.000				
WCP	0.408	-0.189	0.388	-0.048	1.000			
TCM	-0.103	-0.171	-0.143	0.127	-0.234	1.000		
DMAI	-0.528	0.045	-0.692	-0.048	-0.218	0.414	1.000	
SAI	0.570	-0.099	0.678	0.139	0.802	-0.450	-0.659	1.000

Seed in Leaflitter

Table B5:
Results of model 2 in the 95% confidence set with seed in the leaflitter as response variable, with data analysed with a Generalized linear mixed model fit by the Laplace approximation for a poisson distribution

Fixed effect	Estimate ± SE	z-value	p-value
Intercept	-1.10 ± 4.18	-0.26	0.792
Tree Diameter	0.35 ± 0.05	6.54	$6.03e^{-11}$
DMAI	0.15 ±0.07	2.14	0.032
WCP	-0.11 ± 0.04	-2.69	0.007
TCM	-0.43 ± 0.18	-2.39	0.017
Sand Fraction	0.07 ± 0.03	2.25	0.024

Model AIC value: 46 210;Model deviance: 46 186; Random effects: Site, StDev = 1.35; Season 2, StDev = 0.89; Season 3, StDev = 1.75; Sitefactor: 23

Table B6:
Results of model 3 in the 95% confidence set with seed in the leaflitter as response variable, with data analysed with a Generalized linear mixed model fit by the Laplace approximation for a poisson distribution

Fixed effect	Estimate ± SE	z-value	p-value
Intercept	-1.16 ± 4.21	-0.28	0.782
Tree Diameter	0.36 ± 0.05	6.69	$2.26e^{-11}$
DMAI	0.17 ±0.07	2.41	0.016
WCP	-0.12 ± 0.04	-2.91	0.004
TCM	-0.44 ± 0.18	-2.45	0.014
Sand Fraction	0.07 ± 0.03	2.36	0.018
Season 2	0.21 ± 0.19	1.07	0.285
Season 3	0.63 ± 0.33	1.90	0.058

Model AIC value: 46 211;Model deviance: 46 183; Random effects: Site, StDev = 1.40; Season 2, StDev = 0.87; Season 3, StDev = 1.52; Sitefactor: 23

Table B7:
Results of model 4 in the 95% confidence set with seed in the leaflitter as response variable, with data analysed with a Generalized linear mixed model fit by the Laplace approximation for a poisson distribution

Fixed effect	Estimate ± SE	z-value	p-value
Intercept	2.88 ± 4.52	0.64	0.524
Tree Diameter	0.34 ± 0.06	5.88	$4.15e^{-9}$
SAI	-2.09 ±0.95	-2.19	0.029
TCM	-0.44 ± 0.20	-2.21	0.027
Sand Fraction	0.08 ± 0.04	2.25	0.025
Season 2	0.15 ± 0.19	0.77	0.444
Season 3	0.63 ± 0.33	1.81	0.070

Model AIC value: 46 212;Model deviance: 46 186; Random effects: Site, StDev = 1.34; Season 2, StDev = 0.87; Season 3, StDev = 1.53; Sitefactor: 23

Table B8:
Results of model 5 in the 95% confidence set with seed in the leaflitter as response variable, with data analysed with a Generalized linear mixed model fit by the Laplace approximation for a poisson distribution

Fixed effect	Estimate ± SE	z-value	p-value
Intercept	1.03 ± 5.30	0.195	0.845
Tree Diameter	0.35 ± 0.06	5.87	$4.36e^{-9}$
DMAI	0.05 ±0.07	0.72	0.470
SAI	-1.93 ± 0.96	-2.00	0.045
TCM	-0.48 ± 0.20	-2.39	0.017
Sand Fraction	0.08 ± 0.35	2.40	0.017

Model AIC value: 46 212;Model deviance: 46 188; Random effects: Site, StDev = 1.32; Season 2, StDev = 0.90; Season 3, StDev = 1.75; Sitefactor: 23

Table B9:
Results of model 6 in the 95% confidence set with seed in the leaflitter as response variable, with data analysed with a Generalized linear mixed model fit by the Laplace approximation for a poisson distribution

Fixed effect	Estimate ± SE	z-value	p-value
Intercept	-1.43 ± 4.28	-0.34	0.738
Tree Diameter	0.36 ± 0.06	6.21	$5.37e^{-10}$
Tree Density	0.09 ± 0.23	0.41	0.683
DMAI	0.15 ± 0.07	2.07	0.039
WCP	-0.11 ± 0.04	-2.61	0.009
TCM	-0.41 ± 0.18	-2.22	0.027
Sand Fraction	0.07 ± 0.03	2.17	0.030

Model AIC value: 46 212;Model deviance: 46 186; Random effects: Site, StDev = 1.33; Season 2, StDev = 0.90; Season 3, StDev = 1.74; Sitefactor: 23

Table B10:
Results of model 7 in the 95% confidence set with seed in the leaflitter as response variable, with data analysed with a Generalized linear mixed model fit by the Laplace approximation for a poisson distribution.

Fixed effect	Estimate ± SE	z-value	p-value
Intercept	-1.48 ± 4.31	-0.34	0.732
Tree Diameter	0.37 ± 0.06	6.34	$2.27e^{-10}$
Tree Density	0.09 ± 0.23	0.39	0.699
DMAI	0.17 ± 0.07	2.31	0.021
WCP	-0.12 ± 0.04	-2.83	0.005
TCM	-0.42 ± 0.19	-2.27	0.023
Sand Fraction	0.07 ± 0.03	2.17	0.023
Season 2	0.20 ± 0.19	1.03	0.303
Season 3	0.63 ± 0.33	1.90	0.058

Model AIC value: 46 213;Model deviance: 46 183; Random effects: Site, StDev = 1.39; Season 2, StDev = 0.87; Season 3, StDev = 1.52; Sitefactor: 23

Table B11:
Results of model 8 in the 95% confidence set with seed in the leaflitter as response variable, with data analysed with a Generalized linear mixed model fit by the Laplace approximation for a poisson distribution.

Fixed effect	Estimate ± SE	z-value	p-value
Intercept	1.18 ± 5.38	0.22	0.827
Tree Diameter	0.36 ± 0.06	6.00	$2.02e^{-9}$
DMAI	0.06 ± 0.08	0.82	0.411
SAI	-2.09 ± 0.98	-2.14	0.033
TCM	-0.49 ± 0.20	-2.43	0.015
Sand Fraction	0.09 ± 0.04	2.50	0.013
Season 2	0.17 ± 0.19	0.87	0.382
Season 3	0.61 ± 0.33	1.84	0.067

Model AIC value: 46 213;Model deviance: 46 185; Random effects: Site, StDev = 1.36; Season 2, StDev = 0.87; Season 3, StDev = 1.53; Sitefactor: 23

Table B12:
Results of model 9 in the 95% confidence set with seed in the leaflitter as response variable, with data analysed with a Generalized linear mixed model fit by the Laplace approximation for a poisson distribution.

Fixed effect	Estimate ± SE	z-value	p-value
Intercept	0.60 ± 5.35	0.11	0.910
Tree Diameter	0.36 ± 0.06	5.68	$1.35e^{-8}$
Tree Density	0.16 ± 0.23	0.67	0.506
DMAI	0.05 ± 0.07	0.69	0.492
SAI	-1.91 ± 0.97	-1.98	0.048
TCM	-0.45 ± 0.20	-2.20	0.028
Sand Fraction	0.08 ± 0.04	2.31	0.021

Model AIC value: 46 214;Model deviance: 46 188; Random effects: Site, StDev = 1.31; Season 2, StDev = 0.90; Season 3, StDev = 1.75; Sitefactor: 23

Table B13:
Results of model 10 in the 95% confidence set with seed in the leaflitter as response variable, with data analysed with a Generalized linear mixed model fit by the Laplace approximation for a poisson distribution.

Fixed effect	Estimate ± SE	z-value	p-value
Intercept	-1.72 ± 4.40	-0.39	0.696
Tree Diameter	0.36 ± 0.06	6.19	$6.05e^{-10}$
Tree Density	0.09 ± 0.23	0.39	0.695
DMAI	0.13 ± 0.09	1.48	0.140
WCP	-0.11 ± 0.04	-2.37	0.018
TCM	-0.40 ± 0.19	-2.12	0.034
Soil penetribility	-0.01 ± 0.02	-0.29	0.772
Sand Fraction	0.07 ± 0.03	2.12	0.034

Model AIC value: 46 214;Model deviance: 46 186; Random effects: Site, StDev = 1.33; Season 2, StDev = 0.89; Season 3, StDev = 1.74; Sitefactor: 23

Table B14:
Results of model 11 in the 95% confidence set with seed in the leaflitter as response variable, with data analysed with a Generalized linear mixed model fit by the Laplace approximation for a poisson distribution

Fixed effect	Estimate ± SE	z-value	p-value
Intercept	0.71 ± 5.43	0.13	0.896
Tree Diameter	0.38 ± 0.06	5.80	$6.70e^{-9}$
Tree Density	0.17 ± 0.24	0.70	0.484
DMAI	0.06 ± 0.08	0.77	0.444
SAI	-2.06 ± 0.98	-2.10	0.036
TCM	-0.46 ± 0.21	-2.22	0.026
Sand Fraction	0.09 ± 0.04	2.39	0.017
Season 2	0.16 ± 0.20	0.83	0.408
Season 3	0.62 ± 0.33	1.86	0.064

Model AIC value: 46 215;Model deviance: 46 185; Random effects: Site, StDev = 1.34; Season 2, StDev = 0.87; Season 3, StDev = 1.53; Sitefactor: 23

Seed in the soil

Table B16:
Results of model 2 in the 95% confidence set with seed in the soil as response variable, with data analysed with a Generalized linear mixed model fit by the Laplace approximation for a poisson distribution

Fixed effect	Estimate ± SE	z-value	p-value
Intercept	2.62 ± 0.75	3.51	0.0004
Tree Diameter	0.09 ± 0.02	5.78	$7.47e^{-9}$
DMAI	-0.06 ± 0.03	-2.10	0.036
Soil penetrability	-0.02 ± 0.01	-2.23	0.026
Season 2	-0.09 ± 0.11	-0.85	0.395
Season 3	0.29 ± 0.09	3.23	0.001

Model AIC value: 48 446;Model deviance: 48 422; Random effects: Site, StDev = 0.95; Season 2, StDev = 0.54; Season 3, StDev = 0.45; Sitefactor: 25

Table B17:
Results of model 3 in the 95% confidence set with seed in the soil as response variable, with data analysed with a Generalized linear mixed model fit by the Laplace approximation for a poisson distribution

Fixed effect	Estimate ± SE	z-value	p-value
Intercept	-1.69 ± 1.42	-1.19	0.2338
Tree Diameter	0.09 ± 0.02	5.68	$1.38e^{-9}$
SAI	0.63 ± 0.31	2.03	0.043
Soil penetrability	-0.01 ± 0.01	-1.93	0.053
Season 2	-0.09 ± 0.11	-0.86	0.392
Season 3	0.29 ± 0.09	3.22	0.001

Model AIC value: 48 446;Model deviance: 48 422; Random effects: Site, StDev = 0.90; Season 2, StDev = 0.54; Season 3, StDev = 0.45; Sitefactor: 25

Table B18:
Results of model 4 in the 95% confidence set with seed in the soil as response variable, with data analysed with a Generalized linear mixed model fit by the Laplace approximation for a poisson distribution

Fixed effect	Estimate ± SE	z-value	p-value
Intercept	0.18 ± 1.88	0.10	0.922
Tree Diameter	0.09 ± 0.02	5.82	$6e^{-9}$
DMAI	-0.05 ± 0.03	-1.46	0.145
SAI	0.45 ± 0.33	1.39	0.163
Soil penetrability	-0.02 ± 0.01	-2.58	0.010
Season 2	-0.09 ± 0.11	-0.86	0.392
Season 3	0.29 ± 0.09	3.23	0.001

Model AIC value: 48 446;Model deviance: 48 420; Random effects: Site, StDev = 0.92; Season 2, StDev = 0.54; Season 3, StDev = 0.45; Sitefactor: 25

Table B19:
Results of model 5 in the 95% confidence set with seed in the soil as response variable, with data analysed with a Generalized linear mixed model fit by the Laplace approximation for a poisson distribution

Fixed effect	Estimate ± SE	z-value	p-value
Intercept	-0.89 ± 2.07	-0.43	0.668
Tree Diameter	0.07± 0.02	4.41	$1.05e^{-5}$
Tree Density	0.14 ± 0.08	1.69	0.092
DMAI	-0.05 ± 0.03	-1.89	0.059
SAI	0.88 ± 0.34	2.61	0.009
TCM	0.15 ± 0.07	2.17	0.030
Soil penetrability	-0.02 ± 0.01	-2.54	0.011
Sand Fraction	-0.02 ± 0.01	-1.82	0.068
Season 2	-0.10 ± 0.11	-0.87	0.383
Season 3	0.29 ± 0.09	3.24	0.001

Model AIC value: 48 447;Model deviance: 48 415; Random effects: Site, StDev = 0.89; Season 2, StDev = 0.54; Season 3, StDev = 0.45; Sitefactor: 25

Table B20:
Results of model 6 in the 95% confidence set with seed in the soil as response variable, with data analysed with a Generalized linear mixed model fit by the Laplace approximation for a poisson distribution

Fixed effect	Estimate ± SE	z-value	p-value
Intercept	-0.19 ± 2.12	-0.09	0.930
Tree Diameter	0.07 ± 0.02	4.06	$4.92e^{-5}$
DMAI	-0.05 ± 0.03	-1.67	0.094
SAI	0.80 ± 0.35	2.31	0.021
TCM	0.11 ± 0.07	1.70	0.090
Soil penetrability	-0.02 ± 0.01	-2.49	0.013
Sand Fraction	-0.02 ± 0.01	-1.66	0.097
Season 2	-0.09 ± 0.11	-0.85	0.394
Season 3	0.29 ± 0.09	3.23	0.001

Model AIC value: 48 447;Model deviance: 48 417; Random effects: Site, StDev = 0.89; Season 2, StDev = 0.54; Season 3, StDev = 0.45; Sitefactor: 25

Table B21:
Results of model 7 in the 95% confidence set with seed in the soil as response variable, with data analysed with a Generalized linear mixed model fit by the Laplace approximation for a poisson distribution

Fixed effect	Estimate ± SE	z-value	p-value
Intercept	1.05 ± 0.28	3.75	0.0002
Tree Diameter	0.09 ± 0.02	5.68	$1.34e^{-8}$
Season 2	-0.09 ± 0.11	-0.86	0.390
Season 3	0.29 ± 0.09	3.20	0.001

Model AIC value: 48 447;Model deviance: 48 427; Random effects: Site, StDev = 0.89; Season 2, StDev = 0.54; Season 3, StDev = 0.45; Sitefactor: 25

Table B22:
Results of model 8 in the 95% confidence set with seed in the soil as response variable, with data analysed with a Generalized linear mixed model fit by the Laplace approximation for a poisson distribution

Fixed effect	Estimate ± SE	z-value	p-value
Intercept	-0.66 ± 1.25	-0.53	0.600
Tree Diameter	0.08 ± 0.02	5.09	$3.52e^{-7}$
SAI	0.36 ± 0.26	1.38	0.167
Season 2	-0.10 ± 0.11	-0.87	0.383
Season 3	0.29 ± 0.09	3.20	0.001

Model AIC value: 48 447;Model deviance: 48 425; Random effects: Site, StDev = 0.85; Season 2, StDev = 0.54; Season 3, StDev = 0.45; Sitefactor: 25

Table B23:
Results of model 9 in the 95% confidence set with seed in the soil as response variable, with data analysed with a Generalized linear mixed model fit by the Laplace approximation for a poisson distribution

Fixed effect	Estimate ± SE	z-value	p-value
Intercept	-1.16 ± 2.14	-0.54	0.587
Tree Diameter	0.09 ± 0.01	5.90	$3.74e^{-9}$
DMAI	-0.05 ± 0.03	-1.71	0.087
SAI	0.65 ± 0.35	1.83	0.068
TCM	0.08 ± 0.07	1.21	0.226
Soil penetrability	-0.02 ± 0.01	-2.93	0.003
Season 2	-0.09 ± 0.11	-0.85	0.393
Season 3	0.29 ± 0.09	3.23	0.001

Model AIC value: 48 447;Model deviance: 48 419; Random effects: Site, StDev = 0.92; Season 2, StDev = 0.54; Season 3, StDev = 0.45; Sitefactor: 25

Table B24:
Results of model 10 in the 95% confidence set with seed in the soil as response variable, with data analysed with a Generalized linear mixed model fit by the Laplace approximation for a poisson distribution.

Fixed effect	Estimate ± SE	z-value	p-value
Intercept	0.61 ± 1.29	0.47	0.637
Tree Diameter	0.09 ± 0.02	5.98	$2.29e^{-9}$
Tree Density	0.08 ± 0.08	1.00	0.315
DMAI	-0.06 ± 0.03	-2.19	0.029
SAI	0.03 ± 0.02	1.68	0.092
Soil penetrability	-0.02 ± 0.01	-2.48	0.013
Season 2	-0.10 ± 0.11	-0.87	0.387
Season 3	0.29 ± 0.09	3.23	0.001

Model AIC value: 48 447;Model deviance: 48 419; Random effects: Site, StDev = 0.90; Season 2, StDev = 0.54; Season 3, StDev = 0.44; Sitefactor: 25

Table B25:
Results of model 11 in the 95% confidence set with seed in the soil as response variable, with data analysed with a Generalized linear mixed model fit by the Laplace approximation for a poisson distribution.

Fixed effect	Estimate ± SE	z-value	p-value
Intercept	-0.40 ± 1.43	-0.28	0.7819
Tree Diameter	0.09 ± 0.01	6.28	$3.32e^{-10}$
Tree Density	0.13 ± 0.09	1.55	0.122
DMAI	-0.08 ± 0.03	-2.67	0.008
WCP	0.03 ± 0.02	2.14	0.032
TCM	0.09 ± 0.07	1.42	0.155
Soil penetrability	-0.02 ± 0.01	-2.82	0.005
Season 2	-0.10 ± 0.11	-0.87	0.385
Season 3	0.29 ±0.09	3.23	0.001

Model AIC value: 48 447;Model deviance: 48 417; Random effects: Site, StDev = 0.90; Season 2, StDev = 0.54; Season 3, StDev = 0.45; Sitefactor: 25

Seed in the seedbank

Table B27:
Results of model 2 in the 95% confidence set with seedbank as response variable, with data analysed with a Generalized linear mixed model fit by the Laplace approximation for a poisson distribution

Fixed effect	Estimate ± SE	z-value	p-value
Intercept	5.61 ± 1.27	4.44	$9.17e^{-6}$
Tree Diameter	0.08 ± 0.02	5.04	$4.74e^{-7}$
SAI	0.37 ± 0.27	1.40	0.161
Season 2	-0.06 ± 0.11	-0.57	0.570
Season 3	0.36 ± 0.09	3.80	0.0001

Model AIC value: 24647078; Model deviance: 24647056; Random effects: Site, StDev = 0.82; Season 2, StDev = 0.53; Season 3, StDev = 0.47; Sitefactor: 25

Table B28:
Results of model 3 in the 95% confidence set with seedbank as response variable, with data analysed with a Generalized linear mixed model fit by the Laplace approximation for a poisson distribution

Fixed effect	Estimate ± SE	z-value	p-value
Intercept	7.97 ± 0.6	13.34	$< 2e^{-16}$
Tree Diameter	0.09 ± 0.02	5.15	$2.68e^{-7}$
DMAI	-0.03 ± 0.03	-1.17	0.243
Season 2	-0.06 ± 0.11	-0.56	0.575
Season 3	0.36 ± 0.09	3.84	0.0001

Model AIC value: 24647078; Model deviance: 24647056; Random effects: Site, StDev = 0.85; Season 2, StDev = 0.54; Season 3, StDev = 0.47; Sitefactor: 25

Table B29:
Results of model 4 in the 95% confidence set with seedbank as response variable, with data analysed with a Generalized linear mixed model fit by the Laplace approximation for a poisson distribution

Fixed effect	Estimate ± SE	z-value	p-value
Intercept	4.98 ± 1.48	3.37	0.001
Tree Diameter	0.09 ± 0.02	5.30	$1.15e^{-7}$
SAI	0.54 ± 0.33	1.66	0.097
Soil penetrability	-0.01 ± 0.01	-1.18	0.237
Season 2	-0.06 ± 0.11	-0.56	0.574
Season 3	0.36 ± 0.09	3.81	0.0001

Model AIC value: 24647079; Model deviance: 24647055; Random effects: Site, StDev = 0.85; Season 2, StDev = 0.54; Season 3, StDev = 0.47; Sitefactor: 25

Table B30:
Results of model 5 in the 95% confidence set with seedbank as response variable, with data analysed with a Generalized linear mixed model fit by the Laplace approximation for a poisson distribution

Fixed effect	Estimate ± SE	z-value	p-value
Intercept	8.58 ± 0.79	10.81	$< 2e^{-16}$
Tree Diameter	0.09 ± 0.02	5.39	$7.24e^{-8}$
DMAI	-0.05 ± 0.03	-1.59	0.111
Soil penetrability	-0.01 ± 0.01	-1.30	0.195
Season 2	-0.06 ± 0.11	-0.56	0.573
Season 3	0.36 ± 0.09	3.81	0.0001

Model AIC value: 24647079; Model deviance: 24647055; Random effects: Site, StDev = 0.88; Season 2, StDev = 0.54; Season 3, StDev = 0.47; Sitefactor: 25

Table B31:
Results of model 6 in the 95% confidence set with seedbank as response variable, with data analysed with a Generalized linear mixed model fit by the Laplace approximation for a poisson distribution

Fixed effect	Estimate ± SE	z-value	p-value
Intercept	7.10 ± 1.41	5.02	$5.14e^{-7}$
Tree Diameter	0.09 ± 0.02	5.42	$6.07e^{-8}$
DMAI	-0.05 ± 0.03	-1.58	0.115
WCP	0.02 ± 0.02	1.22	0.224
Soil penetrability	-0.01 ± 0.01	-1.49	0.137
Season 2	-0.06 ± 0.11	-0.56	0.577
Season 3	0.36 ± 0.09	3.81	0.0001

Model AIC value: 24647079; Model deviance: 24647053; Random effects: Site, StDev = 0.85; Season 2, StDev = 0.54; Season 3, StDev = 0.47; Sitefactor: 25

Table B32:
Results of model 7 in the 95% confidence set with seedbank as response variable, with data analysed with a Generalized linear mixed model fit by the Laplace approximation for a poisson distribution

Fixed effect	Estimate ± SE	z-value	p-value
Intercept	6.43 ± 2.01	3.21	0.001
Tree Diameter	0.09 ± 0.02	5.35	$8.74e^{-8}$
DMAI	-0.04 ± 0.03	-1.05	0.296
SAI	0.40 ± 0.35	1.15	0.249
Soil penetrability	-0.01 ± 0.01	-1.57	0.115
Season 2	-0.06 ± 0.11	-0.57	0.571
Season 3	0.36 ± 0.09	3.81	0.0001

Model AIC value: 24647080; Model deviance: 24647054; Random effects: Site, StDev = 0.86; Season 2, StDev = 0.54; Season 3, StDev = 0.47; Sitefactor: 25

Table B33:
Results of model 8 in the 95% confidence set with seedbank as response variable, with data analysed with a Generalized linear mixed model fit by the Laplace approximation for a poisson distribution

Fixed effect	Estimate ± SE	z-value	p-value
Intercept	6.84 ± 1.43	4.80	$1.63e^{-6}$
Tree Diameter	0.09 ± 0.02	5.49	$4.03e^{-8}$
Tree Density	0.09 ± 0.09	0.97	0.331
DMAI	-0.05 ± 0.03	-1.61	0.108
WCP	0.02 ± 0.02	1.28	0.200
Soil penetrability	-0.01 ± 0.01	-1.39	0.164
Season 2	-0.06 ± 0.11	-0.56	0.579
Season 3	0.36 ± 0.09	3.82	0.0001

Model AIC value: 24647081; Model deviance: 24647053; Random effects: Site, StDev = 0.85; Season 2, StDev = 0.54; Season 3, StDev = 0.47; Sitefactor: 25

Table B34:
Results of model 9 in the 95% confidence set with seedbank as response variable, with data analysed with a Generalized linear mixed model fit by the Laplace approximation for a poisson distribution

Fixed effect	Estimate ± SE	z-value	p-value
Intercept	6.37 ± 1.99	3.20	0.001
Tree Diameter	0.09 ± 0.02	5.34	$9.51e^{-8}$
Tree Density	0.07 ± 0.09	0.80	0.426
DMAI	-0.04 ± 0.03	-1.08	0.279
SAI	0.38 ± 0.34	1.11	0.268
Soil penetrability	-0.01 ± 0.01	-1.47	0.141
Season 2	-0.06 ± 0.11	-0.56	0.573
Season 3	0.36 ± 0.09	3.80	0.0001

Model AIC value: 24647081; Model deviance: 24647053; Random effects: Site, StDev = 0.87; Season 2, StDev = 0.54; Season 3, StDev = 0.47; Sitefactor: 25

Appendix C

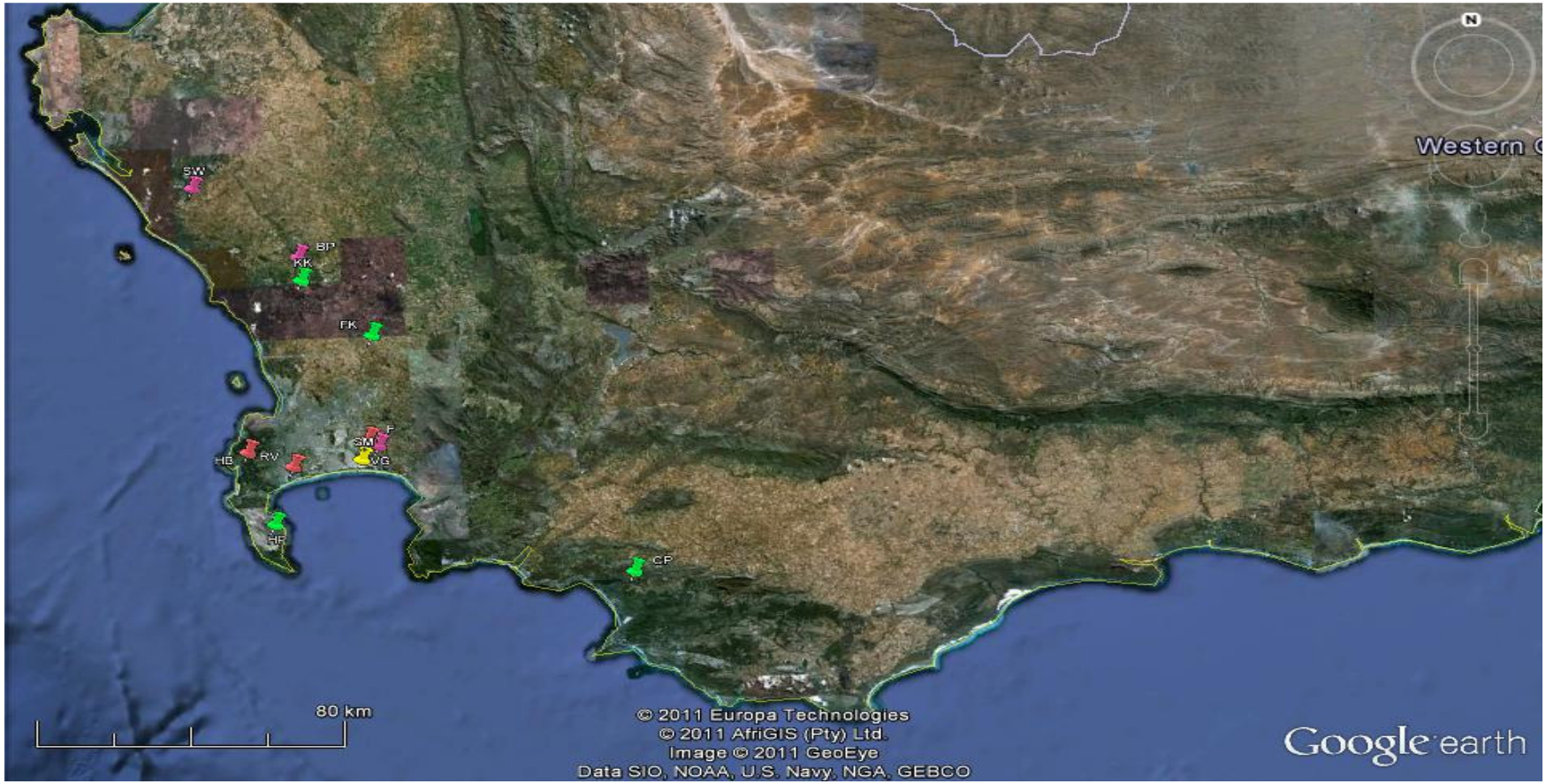

Figure C1: Satellite map indicating position of study sites of previous studies estimating seed rain; Markers of identical colour shows seed rain study sites of same study and year information summarized in table 1

Table C1:
Site information of previous studies estimating seed rain.

Site	Year sampled	Source
Faure (F)	1977	Milton 1980; Milton and Hall 1981
Houtbay (HB)	1977	Milton 1980; Milton and Hall 1981
Rondevlei (R)	1977	Milton 1980; Milton and Hall 1981
Silvermine (SM)	1985	Holmes 1990
Kanonkop (K)	1989	Wood and Morris 2007
Fisantekraal (FK)	1989	Wood and Morris 2007
Hutch's Place (HP)	1989	Wood and Morris 2007
Coppul (CP)	1989	Wood and Morris 2007
Swartwater (SW)	2004	Wood and Morris 2007
Burgerspos (BP)	2004	Wood and Morris 2007
Vergenoegd (VG)	2004	Wood and Morris 2007
Coppul (CP)	2004	Wood and Morris 2007

Appendix D

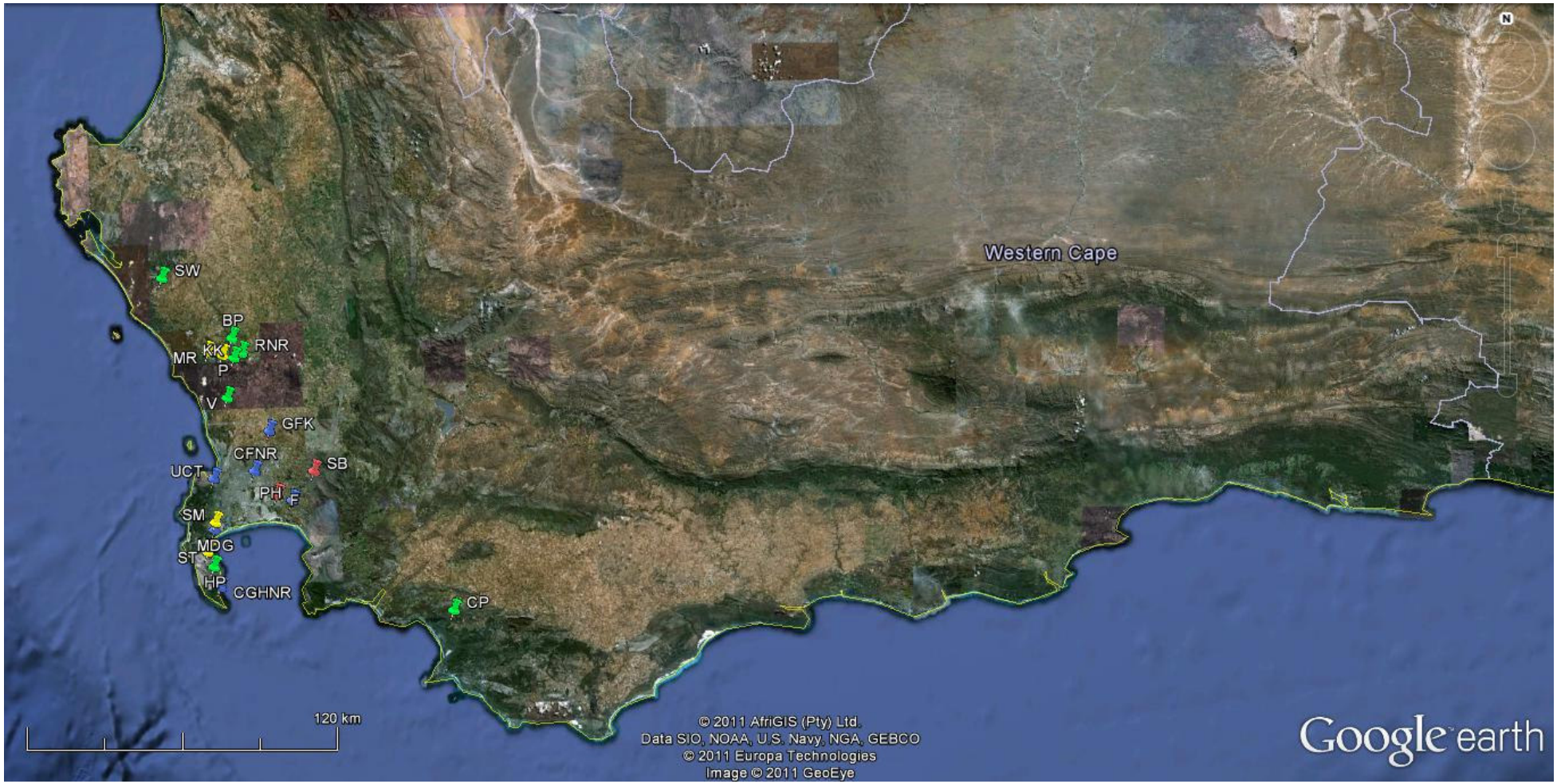

Figure D1: Indicates position of study sites of previous studies estimating seed production. Markers of same colour indicates sites of same study

Table D1:

Site information of previous studies estimating seed production.

Site	Year sampled	Source
Penhill (PH)	1977	Milton 1980; Holmes *et al*., 1987
Faure (F)	1977	Milton 1980
Marina Da Gama (MDG)	1977	Milton 1980
Stellenbosch (SB)	1977	Milton 1980
University of Cape Town (UCT)	1977	Milton 1980
Grootfisantekraal (GFK)	1987	Holmes *et al*., 1987
Cape of Good Hope Nature Reserve (CGHNR)	1987	Holmes *et al*., 1987
Cape Flats Nature Reserve (CFNR)	1987	Holmes *et al*., 1987
Silvermine nature Reserve (SM)	1987	Holmes *et al*., 1987; Holmes *et al*., 2002
Coppul (CP)	1997	Morris 1997
Swartwater (SW)	1997	Morris 1997
Burgerspos (BP)	1997	Morris 1997
Vaaitjie (VT)	1997	Morris 1997
Riverlands (RL)	1997	Morris 1997
Hutch's Place (HP)	1997	Morris 1997
Kanonkop (KK)	1997	Morris 1997
Mamre (MR)	2002	Holmes et al., 2002
Pella (P)	2002	Holmes et al., 2002
Simonstown (ST)	2002	Holmes et al., 2002

Appendix E

Table E1: Large sand fraction (LS) (2 - 0.5 mm), medium sand fraction (MS) (0.5 - 0.25 mm), fine sand fraction (SS) (0.25 - 0.1 mm), very fine sand fraction (VFS) (0.1 - 0.05 mm), large silt fraction (LST) (0.05 - 0.02 mm), fine silt fraction (FST) (0.02 - 0.002 mm) and clay fraction (<0.002 mm) of the soils of 25 *A. saligna* sites.

Site	LS %	MS %	FS %	VFS %	LST %	FST %	Clay %
Rooisand	18	38	27	8	7	1	1
Haasvlakte	22	29	27	11	2	8	1
Moreson	15	25	25	11	12	5	7
Bossiesvlei	19	14	22	23	20	2	0
Romansrivier	20	24	23	11	8	2	12
Veldrift	11	35	34	12	7	0	0
Goudiniweg	12	44	26	8	10	0	1
Citrusdal	15	35	16	6	19	3	7
Travellers Rest	10	30	33	13	10	0	4
Hutchs Place	21	46	19	10	2	0	2
Positano	20	16	16	10	26	12	0
Locheim	20	9	18	18	23	7	5
Swartwater	5	51	32	5	1	4	1
Kragga Kamma	1	8	62	12	9	2	6
Welgelegen	1	20	44	11	18	0	6
Soutvlakte	4	43	40	8	4	0	1
Kanonkop	1	16	73	5	2	0	3
Vergenoegd	8	32	37	10	7	3	1
Rietvlei	8	46	30	13	0	0	2
Coppul	36	13	17	13	15	3	3
Buffelsrivier	16	41	25	8	1	4	5
Fairfield	8	32	35	14	2	6	3
Burgerspos	42	18	25	8	4	1	2
Modderrivier	34	20	34	8	4	0	0
Ysterfontein	0	49	41	6	0	0	4

Appendix F

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Acacia saligna seed banks: sampling methods and dynamics, Western Cape, South Africa

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Abstract

Acacia saligna is potentially the most damaging invasive species in the coastal lowlands of the south-western Cape. The gall rust fungus, *Uromycladium tepperianum*, has been highly successful as a biological control agent for *A. saligna* populations in South Africa and has effectively reduced density, canopy cover and seed production of the tree. However, concerns still remain about the soil-stored seed bank and knowledge of seed bank status and dynamics is crucial for effective management. This study evaluated the effectiveness of two different sampling methods in assessing the status of the seed bank, how the seed bank of *A. saligna* at two different sites varies over time and how these findings compare to findings of other seed bank studies of *A. saligna* across southern Africa. Even with the reduction in seed production caused by biological control, numbers of seed in the soil seed bank are high enough to maintain high levels of recruitment after management or natural disturbances. Both sampling methods (grid and random sampling) attempted were effective in assessing the vertical distribution of the seed bank and estimated the size of the seed bank to be within the same order of magnitude. However, random sampling is more effective in assessing seed bank size as it was found that the seed has a clumped horizontal distribution. The vertical distribution of seed in the seed bank was found to be influenced by soil properties. The largest portion of the seed bank is situated in the upper 10 cm of the soil profile and declines in size with depth.

Keywords: Invasive alien plant, techniques, seed density, spatial distribution

1. Introduction

Introduced species endanger global biodiversity and ecosystem services (Mack et al., 2000; Higgins et al., 1999). Detrimental effects invasive alien species have on the natural environment include reduced species abundance and diversity, species extinctions and changes in nutrient cycling, water availability and fire regimes (D'Antonio and Vitousek, 1992; Richardson et al., 1992; Maron and Connors, 1996; Mack et al., 2000). The fynbos biome in South Africa, renowned for its high species richness (Bond and Goldblatt 1984; Goldblatt and Manning, 2000), is scourged by a whole range of invasive aliens of which *Acacia saligna* (Labill.) Wendl. (Port Jackson willow) is potentially the most damaging in the coastal lowlands of the south-western Cape (Macdonald and Jarman, 1984; van Wilgen and Richardson, 1985).

Indigenous to south Western Australia, this small leguminous tree or shrub (Morris, 1987; Morris, 1991, Cronk and Fuller, 1995), was introduced to South Africa in the mid-nineteenth century to stabilize shifting sand dunes (Shaughnessy, 1980). *Acacia saligna's* success as an invader can be ascribed to a pre-adaptation to a Mediterranean-type climate, a variety of soil types (frequently nutritionally poor) (Witkowski, 1991a; Bell et al. 1993) and periodic fires (Bell et al. 1993). Consequently in the west, south and eastern coastal regions *A. saligna* has formed large dense stands over a vast area on conservation, water catchment and agricultural land (Morris, 1997; 1999). This has resulted in the replacement of natural vegetation, alterations in ecosystem processes and interference with agricultural practices (Morris, 1997, 1999).

In an effort to control the invasion, *Uromycladium tepperianum*, a gall inducing rust fungus, indigenous to Australia, was introduced into *A. saligna* populations in South Africa as a biological control agent. This was done after isolates obtained from *A. saligna* were demonstrated to be host specific (Morris, 1987) and were observed as having detrimental effects to the host plant in its native habitat (Morris, 1997, 1999). *Uromycladium tepperianum* has been highly successful as a bio-control agent as it has resulted in decreased stand density (5-10% of original tree density) (Morris, 1999), reduced canopy density and seed production (Wood and Morris, 2007). In addition a seed-feeding weevil, *Melanterius compactus,* was introduced into *A. saligna* populations in South Africa to compliment the impact of the gall forming fungus and to reduce further the seed production levels of *A. saligna* (Wood and Morris, 2007).

Even with the highly detrimental effects of *U. tepperianum* on *A. saligna*, seed production is still high enough to lead to the accumulation of numerous viable seed in the seed bank and therefore may still be great enough to maintain high levels of recruitment, creating a cause for concern (Morris 1999). *Acacia saligna* seed is approximately 5 - 6 mm in length and 3 - 3.5 mm in width (Doran et al. 1997)

and has an energy content of about 21,9 KJ g^{-1} (King, 1976). Previous studies indicate that *A. saligna* seed maintain high levels of viability in the seed bank, 86.6% (Milton and Hall, 1981) and 86-100% (Holmes et al. 1987). The accumulation of large persistent seed banks in the soil is a consequence of *A. saligna's* seed possessing water-impermeable testas allowing seed to remain dormant in the soil, ensuring their temporal and spatial survival (Rolston, 1978; Holmes et al., 1987). Seed dormancy is broken when the testa is sufficiently damaged to allow water absorption (Milton and Hall, 1981), a process generally initiated by a heat pulse (Tran and Cavanagh, 1984; Jeffery et al., 1988).

Acacia saligna's soil stored seed banks vary in size and are determined by a large number of different factors including seed rain, the age of the stand, stand density or canopy cover, distance from canopy (Richardson and Kluge, 2008), duration of seed dormancy, predation, decay (Weaver and Cavers, 1979; Milton and Hall, 1981), substrate type and degree of soil disturbance (Holmes and Cowling, 1997). The rate of seed accumulation increases with tree age until the trees reach an age of approximately 30 years where after seed accumulation rate stabilizes (Milton and Hall, 1981). The seed banks of *A. saligna* in southern Africa have been recorded as being between 2 000 seeds /m^2 (Morris, 1999) and 212 000 seeds/m^2 (Morris, 1997).

The distribution of seed in the soil profile is influenced by dispersal vectors (e.g. ants and water), soil organisms (e.g. mole rats), substrate type (Milton and Hall, 1981), percolation of water and openings left in the soil for example by decomposing roots (Harper, 1977). *Acacia saligna* seeds are located primarily in the top 8 cm of the soil profile and the seed density has been found to decline rapidly below this level (Milton and Hall, 1981). The nature of the soil will determine how deep seed penetrates into the substrate (Milton and Hall, 1981; Richardson and Kluge, 2008), with seed having been located at a depth of 35 cm in loose sandy soil (Milton and Hall, 1981) and 80 cm in riparian soils (Esler and Boucher, 2004). It has been concluded that horizontal dispersal of Australian acacias is even in southern Africa (Milton and Hall, 1981), while seed of *Acacia* species tends to have a clumped distribution in Australian soils which is attributed to storage of seed by ants in their nests (Majer, 1978). Thus seed density is largest under the canopy of the trees and declines rapidly when moving away from the canopy (Milton and Hall, 1981).

Knowledge of seed bank status and dynamics is crucial for effective management of *A. saligna* and this study contributes to the understanding thereof through:

1. Testing the effectiveness of different sampling methods in assessing the seed bank of *A. saligna*.
2. Evaluating how the seed bank of *A. saligna* at two different sites varies over space and time.
3. Comparing the findings of the two sites to findings of other seed bank studies of *A. saligna* across southern Africa.

2. Methods

Data were collected from two sites, Swartwater and Burgerspos (Table 1) at two sample dates – April 2009 (post-dehiscence) and September 2009 (pre-dehiscence).

2.1. Data collected during April 2009 (Post-dehiscence)

At both sites one 625 m^2 plot was selected in an area with a closed canopy dominated by the target species. In the plot, a grid was established, consisting of five horizontal rows spaced 5 m from each other and five vertical rows spaced 5 m from each other. At every point where the horizontal and vertical lines crossed, a soil sample was taken, giving a total of 25 samples per site.

Soil samples were acquired using a rectangular metal pipe 51.6 cm long and 5 cm wide. The pipe was divided into 5 segments (each 10 cm long, volume of one segment = 0.00025 m^3), separated by 0.4 cm grooves cut horizontally into the pipe. Soil samples were taken to a depth of 40 cm as Esler and Boucher (2004) found the seed of *A. saligna* to be primarily located in the top 0-40 cm of the soil profile. After the soil corer was extracted from the soil, metal plates were inserted into the grooves, dividing the soil in the corer into 4 depth classes: 0-10 cm, 10-20 cm, 20-30 cm and 30-40 cm. The soil of every sample from each depth class was sieved through a 2 mm mesh and the seed counted. The average number of seed for every depth class was calculated. Seed viability was not tested as previous studies (Milton and Hall, 1981; Holmes et al., 1987; Strydom unpublished data) assessed most of the seed to be viable. Data from the two sites for the 0-10 cm depth class were tested for normality and either subjected to a one way ANOVA and/or a Mann-Whitney U test depending on the parametric or non parametric nature of the data.

Data of the 0-10 cm and 10-20 cm depth classes were tested for spatial autocorrelation using Moran's I and Geary's C statistical tests. Moran's I values range from -1 to +1 with -1 indicating even dispersion, 0 random dispersion and +1 clumped dispersion. Geary's C values range from 0 to 2 with 1 indicating random dispersion, <1 clumped dispersion and >1 even dispersion. Spatial autocorrelation tests were only applied to these depth classes as other classes contained too little data to apply meaningful statistics. Furthermore the effect size was calculated to determine the number of samples required to accurately assess the status of the seed bank at different sites.

2.2. Data collected during September 2009 (Pre-dehiscence)

A second set of data were collected during the last week of September 2009 using a different sampling technique. This was done as the effect size derived from data collected during April 2009 (Figure 1) indicated a larger number of independent (i.e. not spatially correlated) samples were needed to accurately assess the status of the seed bank. Independent samples are required since results from the first set of samples showed the distribution of seed in the top soil layer, where most of the seeds are situated, to be clumped. Random sampling is therefore needed to negate the effect of seed aggregation on seed bank data.

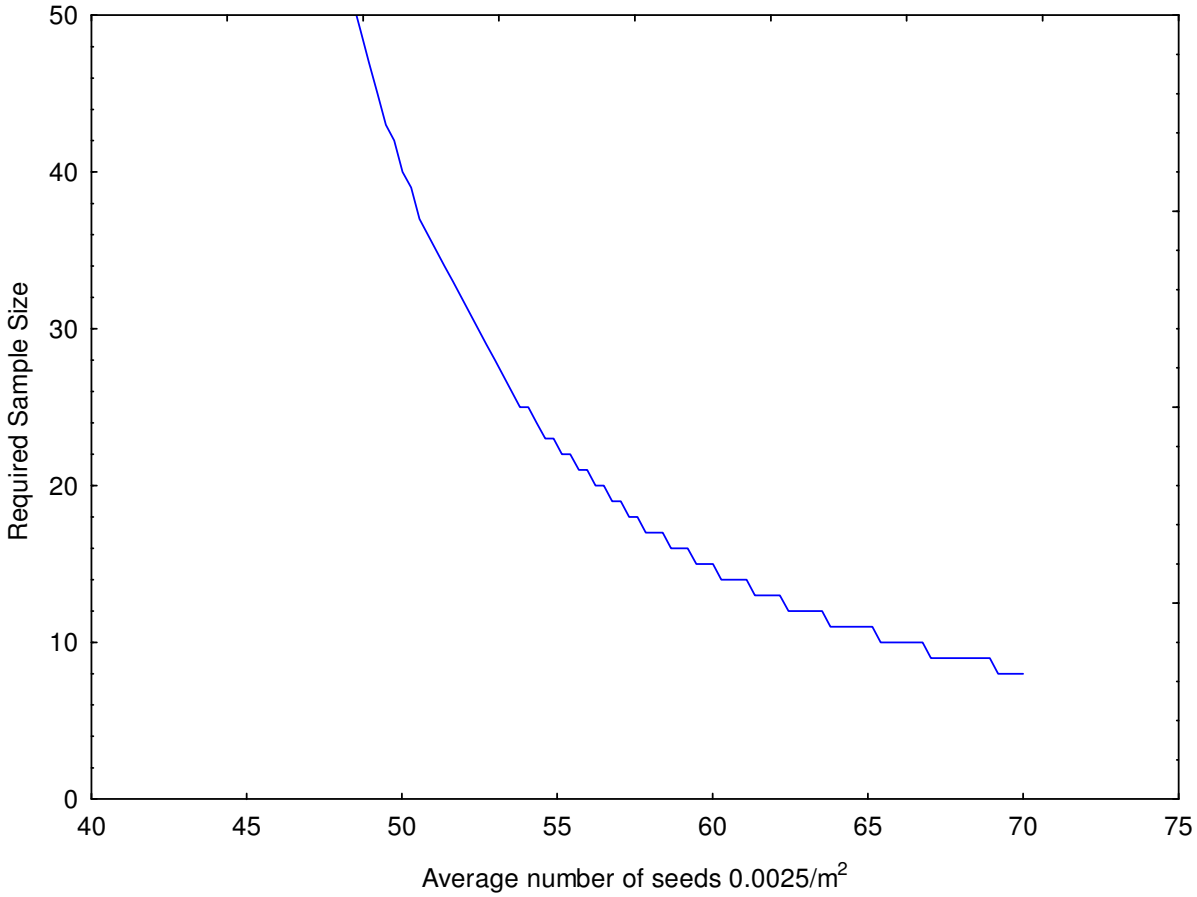

Figure 1. Indicates the effect size which dictates the number of samples required to accurately assess the status of the seed bank for an area. The figure suggests that between 30-50 samples are needed to detect significant differences between the sites sampled in this study [however 30 samples did not detect differences between sites in the second sampling event in September 2009]

A soil corer as described above was used to sample the seed bank during September. Thirty samples were taken at each site at random locations within the *A. saligna* stands. A random number table was used to determine the number of steps (>10 m) and direction of movement between samples. Samples were taken with a soil corer to a depth of 20 cm and were divided into 10 cm and 20 cm depth classes. The soil was sieved through a 2 mm mesh and the seed counted. The average number of seed at each depth for both sites was calculated. Data from the two sites were tested for normality and either subjected to a one way ANOVA and/or a Mann-Whitney U test depending on the parametric or non parametric nature of the data.

At both sites, density of *A. saligna* was determined by counting the number of trees within five randomly placed 5 x 5 m plots and calculating the average. The plots were randomly distributed using the same procedure as above. Furthermore tree density data were tested for normality and either subjected to a one way ANOVA and/or a Mann-Whitney U test depending on the parametric or non parametric nature of the data.

As a proxy for soil depth, relative soil penetrability was assessed by hitting a metal stake (1.5 cm thick) as far as possible into the ground, the distance the stake moved into the earth was measured. This was repeated ten times at every site, and the average depth calculated. These data were tested for normality and either subjected to a one way ANOVA and/or a Mann-Whitney U test depending on the parametric or non parametric nature of the data.

In order to convert data from this study and other studies to number of seed per litre for comparison purposes (as shown in Figure 2), the following formula was used $V=(x\pi r^2/\pi r^2 h)/1000$ for data obtained with a cylindrical shaped corer, and for data sampled with a rectangular shaped corer $V=(xl^2/l^2 h)/1000$. Where V = number of seed per litre; x = seed per m^2; r = radius of the soil core; h = depth of soil core; l = width of soil core.

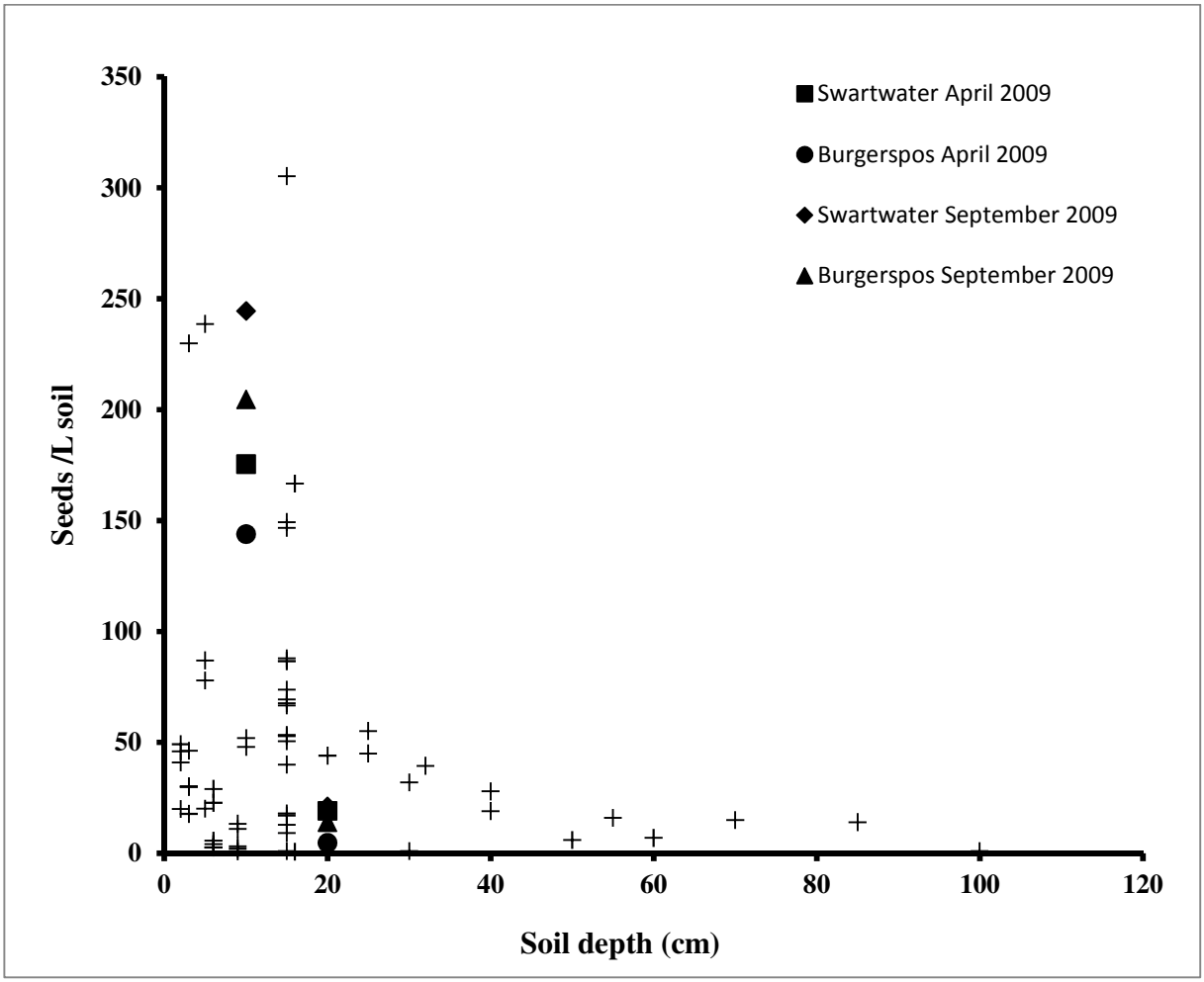

Figure 2. Indicates the vertical distribution of *Acacia saligna* seeds /L soil in the soil at different sites with different vegetation cover and invasion histories. (Data indicated in bold symbols are from this study, additional data were sourced from various other studies listed in Appendix I)

3. Results

3.1. Site Characteristics

The density of *A. saligna* trees at Swartwater is slightly higher than at Burgerspos (Table 1), however, the difference in density between these sites was not significant (ANOVA p-value=0.49). Furthermore the relative penetrability of the soil at Swartwater is greater than at Burgerspos, although the difference is not significant (ANOVA p-value=0.49).

3.2. Seed bank size and vertical seed distribution

When compared to Burgerspos, Swartwater had the largest number of *A. saligna* seed m^{-2} in each depth class for both months sampled (Table 2). However, differences between the 0-10 cm depth class for both methods in each month were not significant (ANOVA p-value=0.37 for April 2009, and =0.22 for September 2009).

Swartwater had a wider vertical seed distribution range than Burgerspos, with Burgerspos having no seed at depths deeper than 20 cm from the soil surface. Furthermore, for both months and sites the largest number of seed was located in the top 0-10 cm of the soil profile.

3.3. Horizontal seed distribution

The Moran's I values (April data, Table 3) for the 0-10 cm depth class were 0.211 and 0.106 for Swartwater and Burgerspos respectively, indicating a clumped distribution pattern for seed in the soil in this depth class at both sites. However, only the Moran's I value of Swartwater (p=0.0098) was found to be significant. The clumped distribution pattern in the 0-10 cm depth class at both sites is further supported by the Geary's C values (Table 3) which were 0.75 for Swartwater and 0.85 for Burgerspos. However, the Geary's C value for both sites for the 0-10 cm depth class was not significant.

Table 1. The location and general characteristics of the study sites Swartwater and Burgerspos

Site	Location	History of invasion	Vegetation Type	General soil type	Gall Rust Fungus Introduction	Tree Density /m^2	Soil penetrability
Swartwater	S 33º 17' E 18º 16'	>20 years	Swartland Granite Renosterveld[1]	Coarse sandy to loamy soils[1]	1988[2]	2.26 ± 0.57	71.5 ± 9.62
Burgerspost	S 33º 31' E 18º 32'	>20 years	Atlantis Sand Fynbos[1]	Grey regic sands[1]	1989[2]	2.01 ± 0.50	69.2 ± 12.30

[1] **Vegetation and general soil type as described by Rebelo et al., (2006)**
[2] **From Morris 1997**

Table 2. Average number (±S.D.) of *Acacia saligna* seeds m^{-2} from different soil profile depths at Swartwater and Burgerspos in April and September 2009

Site	Month	Sampling Method	0-10 cm	10-20 cm	20-30 cm	30-40 cm
Swartwater	April	Grid	17552 ± 9681	1920 ± 4387	144 ± 488	48 ± 132
Burgerspos	April	Grid	14400 ± 8044	480 ± 632	0 ± 0	0 ± 0
Swartwater	September	Random	24452 ± 19676	2108 ± 3408	ND	ND
Burgerspos	September	Random	20468 ± 14628	1400 ± 3392	ND	ND

First number indicates average number of seeds /m^2; second number indicates standard deviation
ND = No Data

Table 3. Moran's I and Geary's C Autocorrelation value for Swartwater and Burgerspos (April 2009)

Site	Depth	Statistic method	Value for Moran's I or Geary's C	p-value
Swartwater	0-10	Moran's I	0.211	0.010
		Geary's C	0.750	0.012
Swartwater	10-20	Moran's I	-0.074	0.747
		Geary's C	1.243	0.952
Burgerspos	0-10	Moran's I	0.106	0.077
		Geary's C	0.851	0.095
Burgerspos	10-20	Moran's I	-0.062	0.578
		Geary's C	0.977	0.420

Table 4. Average number (± S.D.) of *Acacia saligna* seeds m^{-2} at a depth of 15 cm for Swartwater and Burgerspos (Data from Morris 1997). Years when fires occurred, prior to monitoring, are indicated by grey shading, with little impact on seed bank.

Site	Year							
	1991	1992	1993	1994	1995	1996	2009	
Swartwater	3000 ± 1500*	6000 ± 2600	5000 ± 1600	7000 ± 1100	16000 ± 1100	8000 ± 3600	17552 ± 9681	24452 ± 19676
Burgerspos	22000 ± 5100	33000 ± 11000	17000 ± 4900	15000 ± 1300	18000 ± 7200	22000 ± 9800	14400 ± 8044	20468 ± 14628

First First number indicates average number of seeds /m^2; second number indicates standard deviation
First column of 2009 indicates data collected during April 2009
Second column of 2009 indicates data collected during September 2009
*** S.D. data from Morris 1997 has n=4 (each of 10 bulked cores), 2009 data has n=30**

The Moran's I and Geary's C spatial autocorrelation values (Table 3) for both Swartwater (-0.074 and 1.243) and Burgerspos (-0.062 and 0.977) for the 10-20 cm depth class indicate that seeds are randomly distributed within this depth class. However, both the Moran's I andGeary's C values for the 10-20 cm depth class were not significant. The 20-30 cm and 30-40 cm depth classes were not tested with Moran's I and Geary's C tests for spatial autocorrelation as too little seed was present in these depth classes to do meaningful analyses.

3.4. Sampling Methods

Samples acquired during April 2009 were taken post dehiscence whereas samples acquired during September 2009 were sampled pre-dehiscence, yet the average number of seed obtained was substantially larger using the random rather than the grid sampling method at both sites. While different methods were used to retrieve seed from the soil profile in April and September 2009, both methods still indicated that most seeds are located in the top 0-10 cm of the soil and the number of seed decreases as one samples deeper into the soil profile at both sites. However, the standard deviation as a proportion of the mean increased for the random sampling method at both sites for the 0–10 cm depth and at Burgerspos for the 10–20 cm depth. Furthermore the ratios of seed found between Swartwater and Burgerspos remained approximately the same for both sampling methods, these were 1:1.22 and 1:1.19 (Swartwater:Burgerpos) for the grid and random sampling methods respectively.

4. Discussion

To obtain accurate estimates of seed densities of invasive *A. saligna*, two sampling methods for seed banks were compared, providing a basis for future studies. Invasive *A. saligna* presents serious challenges for managers, as significant numbers of seed are still present in upper soil layers, despite the 20 year presence of a destructive biological control agent.

4.1. Grid vs Random sampling

The grid sampling method samples seed in a small area relative to the overall above-ground cover of the *A. saligna* stand. The average seed per unit area is calculated and extrapolated to represent the

seed bank status of the whole stand. The problem with this method is it can miss subtle spatial variation in the seed bank arising for example due to differences in soil profile or in the age of the trees present in the stand (Gross, 1990; Benoit et al., 1992). This can be rectified through increasing the size and number of grid used in the area (Bigwood & Inouye, 1988). A clumped distribution was found for seed in the upper 10 cm of the soil (Table 3). Thus it is possible that aggregations of seed were sampled more than once, this is undesirable as this will lead to over- or under-estimation of the seed bank size (Bigwood & Inouye, 1988; Wiles and Schweizer, 2002). Furthermore, sampling seed banks is a tedious process (Benoit et al., 1992; Wiles and Schweizer, 2002; Ambrosio et al., 2004) and increasing the size of the grids to be sampled dramatically increases the time spent sampling. This method is still effective to attain data on the vertical and horizontal distribution of seed in the seed bank if the grid or grids are representative of the area and if the sample size is adequate. When testing for spatial autocorrelation this method has to be used (Wiles and Schweizer, 2002).

The random sampling method consists of sampling at different, random located points within an area covered by *A. saligna* trees. The average seed per unit area is calculated and assumed to represent the status of the seed bank for the whole area. This method has a higher probability of incorporating horizontal variation in the seed bank as it covers a larger area and also avoids regularly sampling the same aggregation of seed (and therefore over- or under-estimating the seed bank size). Therefore when a clumped spatial pattern is present this sampling method will give a more accurate indication of the seed bank size, but cannot be used to determine any spatial pattern (Wiles and Schweizer, 2002). As this method covers a larger area, the technique requires more samples to be taken. However, the number of samples needed to increase the random sampling techniques' accuracy in determining the size and variation of the seed bank is still less than the number required by the grid sampling method.

This study revealed that, even though the sites varied in habitat characteristics and density of invasion, there were no significant differences in seed bank sizes between sites. However, random sampling revealed larger seed banks with greater variability for both sites than the grid method and therefore random sampling provides a more accurate sampling method to determine seed bank size across entire stands. The seed bank was expected to decline from April (pre-dehiscence) to September (post-dehiscence) due to predation, germination etc. That the opposite was obtained further supports the argument that the former technique is the more accurate method. It may also be possible that within unevenly aged and distributed stands the spatial variation increases.

4.2. Seed bank dynamics in Swartwater and Burgerspos

The current seed bank status of Swartwater and Burgerspos in the top 0-10 cm of the soil for April respectively is comparable to previously published data for these sites (Morris 1997), and confirms previously published data that the majority of seeds are located in the upper part of the soil profile (Milton and Hall, 1981, Holmes, 2002). Morris (1997) bulked 10 samples taken with a soil corer to 15 cm depth at 1 m intervals along each of four close by transects, during April/May, this methodology is comparable to the April 2009 sampling. The seed bank at Swartwater increased significantly in size since 1996 (Table 4). In contrast, the seed bank at Burgerspos showed a trend of decline; however this trend was not significant.

The reason *A. saligna* seed can be found at greater depths at Swartwater than at Burgerspos can be ascribed to the soil of Swartwater having a sandier texture (Milton and Hall, 1981). Decay rates for the seed at Burgerspos reaching soil depths deeper than 20 cm in the soil can also possibly be higher as the water table during winter is very near the soil surface (Personal observation). Furthermore the greater vertical distribution of seed at Swartwater may also be a result of more intense soil organism activity (such as by dune mole rats) or soil disturbance, as has been found in previous research (Weaver and Cavers, 1979; Milton and Hall, 1981; Holmes, 2002). Seedlings of other Australian Acacias, similar to *Acacia saligna* in having seed of comparable size, fail to reach the soil surface and/or are unlikely to establish when germinating below a depth of 10 cm (Pieterse, 1997). However, dormant seed deeper in the soil profile may be moved by soil organisms (Milton and Hall, 1981) to a position within the profile where they are able to emerge if their germination cues are met.

The clumped distribution of seed in the top 0-10 cm of the soil at both sites can be because ants store the seeds in their nests (Milton and Hall, 1981; Holmes, 1990), or possibly because the trees in the area are not uniformly distributed (Milton and Hall, 1981; Holmes et al., 1987; Benoit et al., 1992), or due to the uneven soil surface profile wherein seed accumulates in small dips. The reason for the random distribution of the seed below 10 cm in the soil profile can possibly be because seed movement from the top soil layer is difficult as the soil resistance increases and the fine roots of the trees and other vegetation in this area prevent or decrease the rate of downward movement in the soil. Therefore seed movement is stochastic and can be attributed to the random weakening of one of the factors preventing downward movement in the soil or the random disturbance of these seed aggregations by soil organisms.

There is a trend evident for *A. saligna* stands that indicate, despite different vegetation cover, soil properties and invasion histories, seed banks of *A. saligna* tend to decline in size with depth and the largest portion of the seed banks are situated in the upper 10 cm of the soil (Figure 2).

5. Conclusion

Depending on the required goal of a study, random sampling is possibly the most feasible method for sampling the seed bank as it yields reliable data that are not spatially autocorrelated. Seed banks of *A. saligna* remain a challenge for managers despite the reduction in seed production caused by biological control. Despite different vegetation cover, soil properties and invasion histories, the largest portion of the seed bank is situated in the upper 0-10 cm of the soil and the seed bank declines in size with depth.

Management/ Conservation implications

Despite biological control being present at the study sites for the past 21 years, seed banks are still large and have either increased or remained stable and therefore pose a serious management challenge. This suggests that a single clearing event will not be sufficient for control, and that budgets need to include aspects of managing the seed bank. *A saligna* management will be a long-term commitment.

Soil movement by earthworms and fossorial diggers (e.g. mole rats) will exacerbate this problem by continuous movement of seeds into the deeper soil profile. Although not massive, the seed bank in these deeper layers could be brought to the surface to re-establish *A. saligna* populations.

Acknowledgments

I would like to thank the private landowners and managers of Swartwater and Burgerspos for their assistance and allowing me to conduct my experiments on their property. I am grateful for the field assistance of my father Dr. G.J. Strydom and my classmate J.E.F. Smit, for the help of Prof Martin Kidd with statistical analyses, as well as valuable advice provided Ms J. Moore and F.A.C. Impson from the Plant Protection Research Institute of the Agricultural Research Council. Funding from the South African Association of Botanists, Centre for Invasion Biology and the Working for Water Programme is gratefully acknowledged.

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Appendix I. Information describing locality, methods, data points and data sources used in Figure 2.

Location	Habitat	Treatment	Data collection	Seed /L soil	Source
NA	Riparian, deep sands	Mature, dense, un-burnt stand	1 litre of soil bulked from N=4 samples; collected to depth of 100 cm	46; 78; 52; 45; 19; 16; 15; 14; 1	Boucher and Mortimer 2000
NA	Wetland, sandy	Mature, dense, un-burnt stand, subject to 10yrs biological control	4 bulked samples from 3, 2 x 2 m quadrats to a depth of 60 cm	87; 48; 44; 32; 28; 6; 7	Boucher and Fleitmann 2001
Noordhoek	Wetland, deep sands	Mature, dense, un-burnt stand	30, 5 x 15 cm soil cores taken at each depth to a depth of 30 cm	41; 17; 1	Jasson and Esler 2003
Simonstown	Shallow soils on Table Mountain Group	Previously dense, un-burnt stand, cleared & biomass stacked	30, 5 x 15 cm soil cores taken at each depth to a depth of 30 cm	13	Jasson and Esler 2003
Marina da Gama	Cape flats dune strandveld, soils with a sandy texture	Natural site, short invasion history, Thicket	50, 75 x 150 cm soil cores were taken	0.97	Milton & Hall 1981
Stellenbosch	Clay soil	1 tree,	0.25m^2 pit 5 cm deep	238.64	Milton & Hall 1981
University of Cape Town	Cape flats dune strandveld, soils with a sandy texture	Cleared and burned	100, 75 x 150 cm soil cores were taken	17.96	Milton & Hall 1981
Maitland Cemetery	Cape flats dune strandveld, soils with a sandy texture	Covered with grass, 100yr recurrent thicket	0.25m^2 pit 16 cm deep	0.675	Milton & Hall 1981
Penhill	Swartland granite renosterveld, rock with limited soils	Long history of invasion, cleared	50, 75 x 150 cm soil cores were taken	67.68	Milton & Hall 1981

Appendix I continued

Location	Habitat	Treatment	Data collection	Seed /L soil	Source
Faure	Swartland granite renosterveld, Soils with a marked clay accumulation	Old thicket, history of invasion	50, 75 x 150 cm soil cores were taken	50.57	Milton & Hall 1981
Penhill	Sand plain fynbos, Deep recent sands	Mature, felled & unburnt	20-60, 5 x 15 cm soil cores taken to a depth of 15 cm	69.33	Holmes, MacDonald & Juritz 1987
Grootphisante-kraal	Renosterveld, Clays on Malmesbury shale	Mature, felled & un-burnt	20-60, 5 x 15 cm soil cores taken to a depth of 15 cm	305.33	Holmes, MacDonald & Juritz 1987
Schustersrivier	Strandveld/mountain fynbos, Deep recent sands	Mature, felled, pile & burnt piles	20-60, 5 x 15 cm soil cores taken to a depth of 15 cm	88.00	Holmes, MacDonald & Juritz 1987
Silvermine Nature Reserve	Mesic mountain fynbos, Shallow sand over sandstone	Mature, felled & burnt	20-60, 5 x 15 cm soil cores taken to a depth of 15 cm	52.80	Holmes, MacDonald & Juritz 1987
Cape Flats Nature Reserve	Strandveld/sand plain fynbos mosaic, Deep recent sands	Mature, felled & burnt	20-60, 5 x 15 cm soil cores taken to a depth of 15 cm	149.33	Holmes, MacDonald & Juritz 1987
Coppul	Agulhas limestone fynbos, Greyish, sandy excessively drained soils	Small trees	10, 7 x 15 cm soil core taken to a depth of 15 cm	86.67	Morris 1997
Swartwater	Swartland Granite Renosterveld, coarse sandy to loamy soils	Small trees	10, 7 x 15 cm soil core taken to a depth of 15 cm	53.33	Morris 1997
Kanonkop	Atlantis sand fynbos, Soils with a marked clay accumulation,	Small trees	10, 7 x 15 cm soil core taken to a depth of 15 cm	66.67	Morris 1997
Riverlands	Atlantis sand fynbos, Soils with a marked clay accumulation	Small trees, burned during summers of 1992/1993 and 1993/1994	10, 7 x 15 cm soil core taken to a depth of 15 cm	40.00	Morris 1997

Appendix I continued

Location	Habitat	Treatment	Data collection	Seed /L soil	Source
Hutch's Place	Peninsula sandstone fynbos, rock with limited soils	Small trees	10, 7 x 15 cm soil core taken to a depth of 15 cm	86.67	Morris 1997
Burgerspos (Dense)	Atlantis Sand Fynbos, Grey regic sands	Large trees, burned during summers of 1992/1993	10, 7 x 15 cm soil core taken to a depth of 15 cm	146.67	Morris 1997
Burgerspos (Riverine)	Atlantis Sand Fynbos, Grey regic sands	Large trees, burned during summers of 1994/1995	10, 7 x 15 cm soil core taken to a depth of 15 cm	166.67	Morris 1997
Mamre	Sand plain proteoid fynbos, Quaternary sand 400	Recently invaded, Dense, Un-burnt	Sampling frame, 15 x 15 cm and 5 cm deep. 20 samples taken at three depth levels of 3 cm each	49.17; 20.13; 5.77	Holmes 2002
Pella	Sand plain proteoid fynbos, Quaternary sand 400	Recently invaded, Dense, Un-burnt	Sampling frame, 15 x 15 cm and 5 cm deep. 20 samples taken at three depth levels of 3 cm each	29.93; 22.80; 13.33	Holmes 2002
Silvermine	Mountain proteoid fynbos, Colluvial sandy loam 700	Recently invaded and long invaded sites, Dense, Un-burnt	Sampling frame, 15 x 15 cm and 5 cm deep. 20 samples taken at three depth levels of 3 cm each	46.23; 4.13; 2.07	Holmes 2002
Simonstown	Mountain proteoid fynbos, Colluvial sandy loam 700	Recently invaded and long invaded sites, Dense, Un-burnt	Sampling frame, 15 x 15 cm and 5 cm deep. 20 samples taken at three depth levels of 3 cm each	17.77; 2.80; 3.27	Holmes 2002